Buffering and trophic mismatch in spring-feeding forest caterpillars

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"It would well repay an entomologist, in spite of the temptation, to lay down his net for two or three years and devote his time to hunting the Lepidoptera in their early stages."

J. W. Tutt

1908

Practical Hints for the Field Lepidopterist

Thesis abstract

Across temperate environments, climate warming is leading to a general advancement of spring phenology in a wide range of ecologically and taxonomically diverse species. For taxa that depend on interactions with other species—predators and prey, pollinators, parasites and hosts—widespread phenological changes may cause severe problems. Divergent phenological responses to spring temperature changes among taxa could result in these crucial biotic interactions becoming mistimed. This may cause significant negative fitness effects that could ripple through a population, across trophic levels, and perhaps entire ecosystems. This concept, formalised as the match-mismatch hypothesis (MMH) has become the subject of intense speculation and debate in recent decades.

Much of our understanding of the occurrence and significance of 'phenological mismatch' (negative fitness consequences brought about by mistiming between interacting species) due to climate change comes from the trophic interactions in the classic temperate woodland tree/caterpillar/bird food-chain. This work, however, suffers from many limitations. Spring-feeding caterpillars, forming the central link in this food-chain, are particularly important in that fluctuations in their populations can affect both higher and lower trophic levels. In the tree/caterpillar link, previous literature focuses largely on a single host and caterpillar species pairing: oak (*Quercus robur*) and the winter moth (*Operophtera brumata*). It has been argued that these caterpillars could respond more strongly than their host-plants to climate warming in terms of shifting their phenology, and that even slight mistiming between the two trophic levels has significant negative fitness effects for them. Caterpillars that hatch before bud-burst on their host tree will likely starve, and those that hatch too late are forced to feed on less palatable mature foliage. This rather narrow view, however, overlooks the fact that these caterpillars may be resilient to mistiming in many instances, and that the oak/winter moth trophic interaction may not necessarily be representative of the many other caterpillar species, or alternative host-plant species. In this thesis, I attempt to expand our knowledge and understanding of the operation of the MMH in this system by specifically addressing some of these key caveats.

First, in Chapter 2, in order to address the role of different plant species in the diet of the winter moth and the relative importance of oak as a host-plant species, I consider the effects of host-plant species on survival, growth, and development of the caterpillars, across four British populations. I find that winter moth caterpillar fitness varies substantially across host-plant species, but that there are also strong population-specific responses consistent with genetic divergence. In contrast to the assumptions typically made in the literature that oak is the "primary", "principal", or most significant host-plant species in the field, I find that caterpillar performance on this species is consistently poor relative to other abundant and widespread host-plant species. Reconciling this apparent inconsistency represents an obvious avenue for future research. A taxonomically broad diet may serve to buffer winter moth caterpillars against the effects of mismatch on any one host-plant species—phenology varies across hosts and, averaged across a population, this might ensure there are always some food resources available for individuals to exploit.

Next, in Chapters 3 and 4, to determine whether the impacts of mismatch generalise across caterpillar and host-plant species, I directly test the effects of mistiming across a range of British spring-feeding caterpillar species, including the winter moth. In Chapter 3, I consider the effects of late-hatching asynchrony on performance (and fitness in the winter moth) of up to 65 days. I find that the effects of asynchrony on performance are contingent on the particular caterpillar/host-plant species pairing in question. Depending on the host-plant species, some caterpillar species show little to no decline in performance across a period of several months (e.g. vapourer *Orgyia antiqua* on birch *Betula pendula* or sycamore *Acer pseudoplatanus*), while others show precipitous declines in a matter of days (e.g. fitness in winter moth on sycamore or sallow *Salix caprea*). This highlights the danger of extrapolating from a single caterpillar/host-plant species pairing. Indeed, in both cases, the winter moth and oak appear to be exceptional—performance of the former typically showing a steeper than average decline with increasing asynchrony, and the latter being a generally poor host for most spring-feeding caterpillar species, on which performance declines at a greater rate than other host-plants with asynchrony. Overall, I find that, in contrast to the prevailing view in the literature, synchrony *is* important for caterpillar fitness, but within fairly broad bounds (at a scale of weeks and months, rather than days), though this varies across hosts and species.

In Chapter 4, I consider asynchrony in the opposite direction, and investigate the ability of spring-feeding caterpillars to cope with hatching too early, before bud-burst on their natal tree. Early hatching caterpillars can simply tolerate a lack of food and wait until it becomes available, or they may be able to exploit the unopened buds of their host-plants as a food source in the intervening period. I found that across five spring-feeding caterpillar species, there is often a considerable ability to tolerate starvation, ranging from several days in the winter moth and mottled umber *Erannis defoliaria*, to over thirty in the black arches *Lymantria monacha*. Increased temperatures, however, significantly reduced the time which caterpillars could survive without food, often by a substantial margin (e.g. by twenty days in the black arches moth at temperatures of 21°C versus 5°C). In the winter moth, I show experimentally for the first time that caterpillars are indeed able to feed on the unopened and opening buds of a range of their host-plant species. However, the likelihood of establishment on buds is initially low and increases steeply as buds mature and softer tissue becomes more exposed. Nonetheless, this clearly demonstrates that many spring-feeding caterpillar species have at least some ability to tolerate early hatching on their host tree.

In Chapter 5, I consider in more detail the widely-held assumption that foliage becomes unsuitable for caterpillar consumption very soon after bud-burst. In contrast to Chapter 3, I reared caterpillars on frozen foliage collected from a sample of trees across a two week period after bud-burst, to determine the effects of any changes in their structure and secondary chemistry across this period on palatability. Specifically, I focussed here on the effects of caterpillar asynchrony on growth rate and rate of survival across time, both of which have distinct fitness implications versus overall mass attained or survival probability (cf. Chapter 3). I find no consistent effects of leaf age on rates of mortality across time, suggesting that leaf maturation occurring within the first two weeks after bud-burst generally has little effect on caterpillar performance. There are, however, significant effects of host-plant species and age on growth rates—on older oak foliage, growth rates are higher, the implications of which are unclear. Additionally, I find that there is substantial variation in caterpillar performance between individual trees and broods. Taken together, these findings may indicate that phenological variation between individual trees could serve to ameliorate mismatch, buffering against it at the population level.

Finally, in Chapter 6, I discuss the concept of ‘buffering’ in detail—a phrase widely used but little considered. I argue that buffering is related to concepts of stability in living systems, and that it represents the means by which stability is maintained, via a range of ‘buffering mechanisms’. I define buffering as “*the amelioration of any fitness effects resulting from an environmental change”.* I explore the concept specifically within the spring-feeding caterpillar system, and argue that the very unpredictability and uncertainty that is an inherent part of their niche has driven the evolution of many of the buffering mechanisms by which that variation can be tolerated. By extension, I propose that a predisposition to tolerating environmental uncertainty may mean these species will be buffered against at least some of the negative effects of future climate change, such as an increased incidence of asynchrony.

Taken together, my analyses suggest that the overwhelming focus placed on the winter moth/oak interaction in literature on the MMH is likely to be misleading—these taxa are not necessarily representative of other species at these trophic levels in the woodland food web, and the effects of asynchrony on caterpillar performance and fitness is highly contingent on both taxa involved. It is therefore difficult and perhaps unwise to make excessively broad generalisations about the effects of climate change on the broader spring-feeding caterpillar guild, and any cascading effects to other species with which they interact. Contrary to the widespread view in the literature, the caterpillars of a range of moth species seem able to cope with at least some degree of both early- and late-hatching asynchrony: by feeding on a range of host-plant species; by tolerating more mature foliage; by tolerating starvation when food is unavailable; and, by utilising the young, unopened buds of their host-plants as food. These traits may equally well buffer caterpillars against potential mismatch resulting from divergent phenological responses to future climatic change relative to their host-plants. More broadly, this particular instance highlights the potential general importance of buffering as a phenomenon in other groups of organisms, where it could play a key role in ameliorating some of the negative effects of climate change.

Lay summary

Climate change is affecting the timing of stages in the life cycles of many different species. In spring, for example, species are occurring earlier because of warmer conditions. The extent of these changes can vary across different species, and some are responding more strongly to the warmer conditions than others. For animals and plants that rely on occurring at the same time as another species—such as a predator with a seasonal food source—these changes in timing of different magnitudes can cause problems. One frequently referenced example of this is in the tree/caterpillar/bird food-chain that occurs throughout temperate woodlands. Caterpillars must hatch at the correct time in spring—too early, and the buds on their host trees will still be closed and there will be no food for them to eat; too late and the leaves will be older, tougher and more difficult to consume. In turn, various bird species such as blue and great tits which breed in spring have to lay their eggs at an appropriate time so that their offspring will hatch at the peak of food availability, when caterpillars are at their most abundant. If, in response to climate change, each of these levels shift the time that they occur in spring by different margins, then the species with which they interact with them will be affected. This could be potentially catastrophic across an ecosystem.

In this thesis, I focus on the under-studied caterpillar link in this model food-chain, and the pressures they face to match the timing of buds opening and leaves appearing on their host-plant. I argue that the importance of precisely matching the timing of their host-plants may have been overestimated and that, perhaps due to the unpredictability and variation inherent in the onset of spring, these caterpillars employ a range of mechanisms to help them tolerate mistiming. Spring-feeding caterpillars actually have a very broad diet, and can consume leaves from a wide range of different plants species (Chapters 2 and 3). Because different plant species open their leaves in spring at different times, and are affected by higher temperatures in different ways, this means that even if a caterpillar hatches at the wrong time relative to one host, they may hatch at the correct time relative to another. Previous research in this system has tended to focus on two model species, caterpillars of the winter moth *Operophtera brumata* and oak *Quercus robur*, and generalise from this interaction. However, I show that different caterpillar species often respond very differently to being mistimed with their host-plant—the extent to which they can feed on older, more mature foliage varies substantially (Chapters 3 and 5), as does their ability to endure periods of starvation (Chapter 4). In addition, in the winter moth I show that where caterpillars hatch too early, they are able to bore into the unopened buds of their host-plants and feed on the developing tissue (Chapter 4). Although caterpillars suffer higher mortality, it may be a strategy they can employ to avoid complete starvation. In general, most species show some degree of tolerance to being mistimed, contrary to popular assumption—and some are extremely tolerant of hatching at the wrong time. Importantly, those species which have been the focus for previous research may not be very typical of the responses we see in general: winter moth seems to be particularly susceptible to the negative effects of mistiming with their host-plant (Chapters 3, 4 and 5), and oak would seem to be a relatively poor host (Chapters 2 -5).

Matching the timing of their host-plant is clearly important for spring-feeding caterpillars, but I argue throughout this thesis that they are in many ways also 'buffered' against mistiming (Chapter 6). The 'buffering mechanisms' which help to ameliorate the negative effects of being mistimed—such as being able to feed on underdeveloped buds, or a range of different host-plant species—may have evolved precisely because conditions in spring are difficult to forecast, and individual caterpillars, when they hatch, never know exactly what the environment they face will look like. By extension, these buffering mechanisms may also act to ameliorate the effects of future climate change, if this results in more frequent mistiming between caterpillars and their hosts (Chapter 6). The particular example of spring-feeding caterpillars, and the surprising extent of their resilience in spite of mistiming, might suggest that we re-examine other systems where we assume that timing is important and, in light of predicted future climate change, consider how they may also be buffered against environmental variation and change. Given our justifiable concerns about the pace and extent of predicted climate warming, the pervasiveness of buffering in natural systems could not be more important.

Declaration

I declare that this thesis has been composed solely by myself, with guidance throughout from my primary supervisor Dr Albert Phillimore.

This work has not been submitted, in whole or in part, in any previous application for a degree.

Except where stated otherwise by reference or acknowledgment, the work presented is entirely my own.

Jamie C. Weir

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All science is collaborative, among the living and also with those pioneers of previous generations. This work builds on the elegant and inspirational research of countless entomologists, ecologists and evolutionary biologists, past and present, to whose dedication and enthusiasm we owe what knowledge we have about the natural world.

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Table of Contents

Chapter 1: General introduction

1.1. Climate change and phenology

Average global temperatures are increasing, and both the speed and scale of these changes are unprecedented in thousands of years. Recent temperatures are at their highest levels in over 6500 years (throughout the present interglacial warm period), and have already risen by 1°C from pre-industrial levels (IPCC, 2021). Not only this, but the rate of change is also considerable—since 1970, temperatures have increased at a greater rate than any other comparable period in the last 2000 years (IPCC, 2021). It is predicted that extreme weather events such as droughts, heatwaves, wildfires, heavy rainfall, and tropical cyclones will occur more often in future, as a consequence of these climatic changes (IPCC, 2021). The frequency and severity of these events, as well as future mean global temperatures, are expected to depend on the rates of anthropogenic greenhouse gas output (IPCC, 2021). Global temperatures could increase by an additional 1-1.8°C by the end of the century with dramatically reduced emissions, or by 3.3-5.7°C with increasing rates of emissions (IPCC, 2021). Considering the clear role that greenhouse gases have played as contributory or even decisive factors leading to historical mass extinctions (Taylor, 2004), understanding the effects of present day emissions, their association with modern temperature changes, and the impacts of these climatic changes on species—and natural ecosystems as a whole—is a vitally important ongoing task for modern biology (for a more detailed discussion of the history of the Earth's climate, setting the present changes within context, see Appendix 3).

In temperate environments, climatic conditions such as temperature undergo seasonal cycles which affect species both directly and indirectly. Variation in the suitability of the environment for plant growth, for example, affects a wide range of species directly or indirectly dependent on those plants—phytophagous insects are restricted in their occurrence to periods of availability of plant foliage; secondary consumers such as birds and mammals, dependent on insects as a food resource, are therefore indirectly affected by the plant growing season. Consequently, species often time stages in their life history (their 'phenology') to coincide with predictable abiotic and biotic environmental conditions which are favourable for those stages— trees come into leaf in early spring, when weather conditions become reliably favourable for growth; birds and mammals rear their young in spring as plants grow and food becomes more abundant; insects undergo diapause or hibernation during inhospitable periods of excessively cold (e.g. in N. Europe) or warm (e.g. in the Mediterranean) conditions, usually in specially adapted stages (Leather *et al.*, 1993). A general warming of temperatures, such as we have observed over recent decades, has the effect of shifting the calendar dates on which seasonal conditions change, and pass thresholds of suitability or unsuitability for biological activity of various kinds.

Unsurprisingly, changes in phenology are some of the most well documented biotic responses to recent climate change (e.g. Walther *et al*., 2002; Parmesan and Yohe, 2003; Amano *et al*., 2010; Thackeray *et al*., 2016; Cohen *et al*., 2018; Radchuk *et al*., 2019; Roslin *et al*., 2021). As we might predict from rising mean temperatures, advances in spring phenology have been widely observed, across a range of organisms—that is to say, spring phenological events have been occurring on average at an earlier calendar date than in the past. For example, analysing data from 542 plant species across European phenological recording schemes, Menzel *et al*. (2006) found that the dates of a range of spring and summer phenological events—including leaf bud-burst, flowering, and fruiting, as well as the date of farming events such as harvesting and tilling—showed a close negative correlation with temperature (*r* ranged from 0.45 to 0.66). Averaged across species and events, spring and summer plant phenology advanced by 4.6 days/°C and 2.5 days/decade. These figures have found broad agreement across subsequent studies of plants: 5 days/°C for flowering (Amano *et al.*, 2010), 4-6 days/°C for flowering, 4-9 days/°C for leafing/bud-burst (Wolkovich *et al.*, 2012), 4.1 days/°C averaged across primary producer phenological events (Thackeray *et al.*, 2016), and 1.1-3.3 days/decade across trees, shrub, and herb events (Parmesan, 2007). Menzel *et al*. (2006) found 78% of bud-burst and flowering events showing advancement across time (1951-1999), 31% displaying significant advancement, and 75% of fruiting dates showing advancement, 25% significantly so. Among animals, we find similar evidence for phenological advancement across time due to increased temperatures (Wolkovich *et al.*, 2014; Cohen *et al.*, 2018). Cohen *et al.* (2018) analysed the average spring phenology of animals across 127 long-term study systems since 1950, and found that it had advanced by 2.88 days/decade—a change of similar magnitude to that seen in plants (see above) and other cross-taxa studies (2.7-4 days/decade

[Kharouba *et al*., 2018], 1.9-3.7 days/decade [Thackeray *et al*., 2016], and 2.8 days/decade [Parmesan, 2007]).

There is even some evidence to suggest that phenological change has accelerated, at 4 days/decade since 1981, in comparison to 2.7 days/decade pre-1981 (Kharouba *et al.*, 2018)—this is in line with a recent acceleration of temperature increases (IPCC, 2021). However, some studies seem to illustrate trends in the opposite direction, showing delayed phenological events with increasing spring temperatures (Barbraud and Weimerskirch, 2006; Yu *et al.*, 2010; Lane *et al.*, 2012). This highlights the complex nature of these ecological systems—a theme I shall return to throughout this thesis: the dense networks of inter- and intraspecific interactions and feedback loops, all of which make predicting exactly how a given ecosystem or community will respond to any environmental change very difficult. For example, warmer mean temperatures could reduce the degree of the winter chilling of seeds so that vernalisation is not induced (Yu *et al.*, 2010). In animals this "winter chilling" does not seem to operate as widely (Cohen *et al*., 2018; though cf. various Lepidoptera in Kimberling and Miller, 1988; Hibbard and Elkinton, 2015; Stålhandske *et al*. 2017).

In spite of this overall complexity, there is fundamental agreement on the general direction of these trends—spring events are becoming earlier and some autumn events are becoming later (Menzel *et al.*, 2006; Roslin *et al.*, 2021), consistent with an extension of the growing season (Walther *et al.*, 2002). Within the broad trends of phenological change at the level of higher taxonomic groupings, however, we can see individual species (and even closely related species) responding in very different ways. The slope of mean flowering date against temperature in horse chestnut *Aesculus hippocastanum* is almost twice the magnitude of that in common hazel *Corylus avellana* (B = 0.047 vs 0.028)—that is to say, temperature affects phenology at twice the rate—and explains twice the variance in the phenological data (R^2 = 0.74 vs 0.37) (Myneni *et al.*, 1997; Menzel *et al.*, 2006). Some species have even shown phenological responses to warming in opposite directions at different sites, with different baseline temperature levels—Roslin *et al*. (2021) note that the ripening of fruits on two *Vaccinium* species, for example, has advanced with climate change at relatively colder sites, but has delayed at warmer sites. The effects of climate change on phenology are highly site and taxon dependent, modulated by the complex interactions between other ecological and environmental factors, defying simple characterisation (Roslin *et al.*, 2021). Hence, making robust predictions as to the ecological effects of such changes in future is difficult.

Different phenological responses to climate change among taxa are of particular importance since, for many organisms, successfully timing their phenology involves it being temporally synchronised (see Appendix 6) with the phenology of another species. Certain fish, for example, which fail to spawn at the correct time can find their offspring mismatched with the maximum abundance of their food supply, with deleterious consequences for recruitment to the population (Cushing, 1990). A further example is well illustrated by birds which can suffer reductions in offspring condition (Samplonius *et al.*, 2016), individual fitness (Reed *et al.*, 2013), and perhaps population size (Both et al., 2006; Mclean et al., 2016; though see Samplonius et al., 2020) if they mistime their breeding relative to the maximum availability of an ephemeral food supply. Any negative effects of mistiming on populations at lower trophic levels could possibly ripple up to higher levels (Durant *et al.*, 2005, 2007). Thus, the stability of entire ecosystems may be contingent on the broadly successful timing of interactions between different species and, more generally, trophic levels.

Primary consumers and producers consistently advance their spring phenology in response to climate warming by a greater margin than secondary or tertiary consumers (Walther *et al.*, 2002; Thackeray *et al.*, 2016; Cohen *et al.*, 2018; Kharouba *et al.*, 2018; Roslin *et al.*, 2021). Thackeray *et al*. (2016), for example, found that producers, primary consumers, and secondary consumers advance their phenology by an average of 4.1, 3.7, and 1.9°C/day, respectively. In warmer years, therefore, secondary consumers will lag substantially behind primary producers and consumers in their phenological adjustments. Kharouba et al. (2018), conducting a meta-analysis of reported phenological changes in 54 pairwise predator-prey interactions, found that the relative timing of interacting species had shifted by 6.1 days/decade since the 1980s. For most interactions the size of the change in synchrony was small (<5 days/decade), but in some cases was very large, around 10-15 days/decade (Kharouba *et al.*, 2018). Not all phenological changes result in reduced temporal synchrony, however, some have the opposite effect (Roslin *et al.*, 2021)—indeed, Kharouba *et al.* (2018) found the majority of pairwise predator-prey interactions (57%) occurring closer in time to one another relative to historical comparisons, although, of course, this means that 43% were still occurring further apart. In this case, mistiming raises the possibility of increased interand intra-specific competition among predators which were historically more temporally separated, or increased predation pressure on species at lower trophic levels relative to which consumers (their predators) are now more synchronised.

1.2. Phenological asynchrony and the match-mismatch hypothesis

The idea that the degree of phenological synchrony between a consumer and its resource could directly affect the fitness of that consumer was first properly formalised by the British fisheries and marine biologist David Cushing as the *match-mismatch hypothesis* (henceforth, MMH) (Cushing, 1967, 1969, 1975, 1990). At a simple level, we can break this hypothesis down into two broad, testable components: firstly, that the resource in question shows some degree of ephemerality or seasonality in its availability; secondly, that fitness, recruitment, or some such measure of performance in the consumer taxon is dependent on the availability or abundance of that resource—in the degree to which they match the resource (Durant *et al.*, 2007; Kharouba and Wolkovich, 2020).

The MMH is in essence a very specific case of stabilising selection—it explains the adaptive, concurrent timing of a consumer with its resource. Where the availability of the resource shifts, selection exerted under the MMH can become directional, pushing consumer phenology in the same direction as that resource shift. Climate change, and warmer springs causing phenological advancement, is one way in which these differential shifts may be produced. Although phenological changes and the MMH are frequently invoked as mechanisms by which climate change might negatively affect natural populations, this question has seldom been tested adequately (Samplonius *et al.*, 2020). To clearly establish that climate change-induced phenological changes are negatively affecting the fitness of a population, Samplonius *et al.* (2020) identified five testable criteria:

> “1. An ephemeral resource contributes a large proportion of the consumer’s diet.
>
> 2. Asynchrony between consumer and resource phenology is increasing over time.
>
> 3. Variation in asynchrony is driven by inter-annual variation in temperature.

> 4. Asynchrony impacts negatively on consumer fitness.
>
> 5. Asynchrony impacts negatively on consumer population size, density or growth.” (p157)

Analysing 129 papers in a systematic literature review, Samplonius *et al.* (2020) found that only two studies addressed all five criteria, and 58% considered only two of them. The overwhelming majority of studies (97%) addressed Criterion 1—the dependence of the consumer species on an ephemeral resource—but 74% of these did so only by a simple *a priori* statement or assertion that the resource was important and time-limited. Criterion 2—that the observed asynchrony was increasing over time—was the next most tested criteria, with all the remaining trailing far behind. The fact that the majority of such studies relied simply on pre-existing natural history knowledge of the system in question, and did not explicitly test the *degree* or *extent* of the dependence of the consumer on the particular resource species (or group of taxa or guild) in question, highlights a wider failing in the literature to address the pre-existing, pre-climate change baselines of study systems (Kharouba and Wolkovich, 2020; though see for example Singer and Parmesan, 2010). Understanding these baseline conditions includes a more complete appreciation of the many facets of the ecology and biology of the species in question.

And yet, the current literature on climate change and the MMH shows considerable geographical, taxonomic, and trophic bias—there is an overwhelming focus on secondary consumers, terrestrial systems, and to sites in Europe and North America (almost exclusively in the northern hemisphere) (Durant *et al.*, 2007; Visser *et al.*, 2012; Kharouba and Wolkovich, 2020; Samplonius *et al.*, 2020). We know, however, that the impact of climate on phenology can vary significantly across trophic levels (Thackeray *et al.*, 2016; Cohen *et al.*, 2018; Roslin *et al.*, 2021); that the ecological and trophic forces shaping marine and terrestrial food webs and regulating the populations of marine and terrestrial species are quite distinct (Kharouba and Wolkovich, 2020); and that the recent and ongoing changes in the climate are geographically heterogeneous across the globe (IPCC, 2021). Most aquatic based studies approach the MMH from the community or population perspective and consider the consumer and resource equally, while terrestrial systems focus predominantly on aspects of the individual life history and fitness of the consumer (Kharouba and Wolkovich, 2020).

The idea that climate change is causing differential changes in the phenology of interacting species, such that many species, perhaps even whole ecosystems, are becoming *mismatched*, with potentially catastrophic effects, is compelling but is only patchily supported by the current body of evidence. A little considered fact, for example, is the extent to which the MMH is a specialised phenomenon, perhaps affecting only a very small number of organisms. Aspects of the life history and ecology of many species might render them more or less vulnerable to mismatch, varying across trophic levels, functional groups, and guilds. Nesting birds, for example, rely on temporally narrow windows of food availability while rearing their offspring. In contrast, reptiles are typically generalists, without reliance on an ephemeral food supply; in mammals, females accumulate food stores to help support the rearing of their offspring—in both instances, these taxa are rendered less vulnerable to climate-induced mismatch, precisely because their ecology is such that they are not as reliant on an ephemeral resource (Durant *et al.*, 2007). Even if it occurs only rarely, however, those species or guilds which are affected by the MMH may still be key to the functioning of an ecosystem, or centrally placed within it (Varley *et al.*, 1974). Nonetheless, for such a widespread, widely cited hypothesis, there are serious deficiencies in the evidence underlying it (Kharouba and Wolkovich, 2020; Samplonius *et al.*, 2020).

1.3. Phenological asynchrony in tri-trophic woodland food-chains

With the onset of spring in temperate environments we often see an ephemeral pulse of resource availability, characteristic of ecological situations where the MMH might operate (Figure 1.1). Newly available foliage, particularly on woodland trees, offers an important resource for phytophagous insects. The abundance of arboreal caterpillars undergoes a distinct peak in early spring—just as the buds are beginning to break and the leaves appearing—before rapidly declining (Gibb, 1950; Balen, 1973; Holliday, 1977; Naef-Daenzer and Keller, 1999; Naef-Daenzer *et al.*, 2000; Thomas *et al.*, 2001; Southwood *et al.*, 2004; Charmantier *et al.*, 2008; Smith *et al.*, 2011; van de Pol *et al.*, 2016; Shutt, 2017; Shutt *et al.*, 2019a; Macphie *et al.*, 2020, 2022). The availability of these insects, in turn, represents an

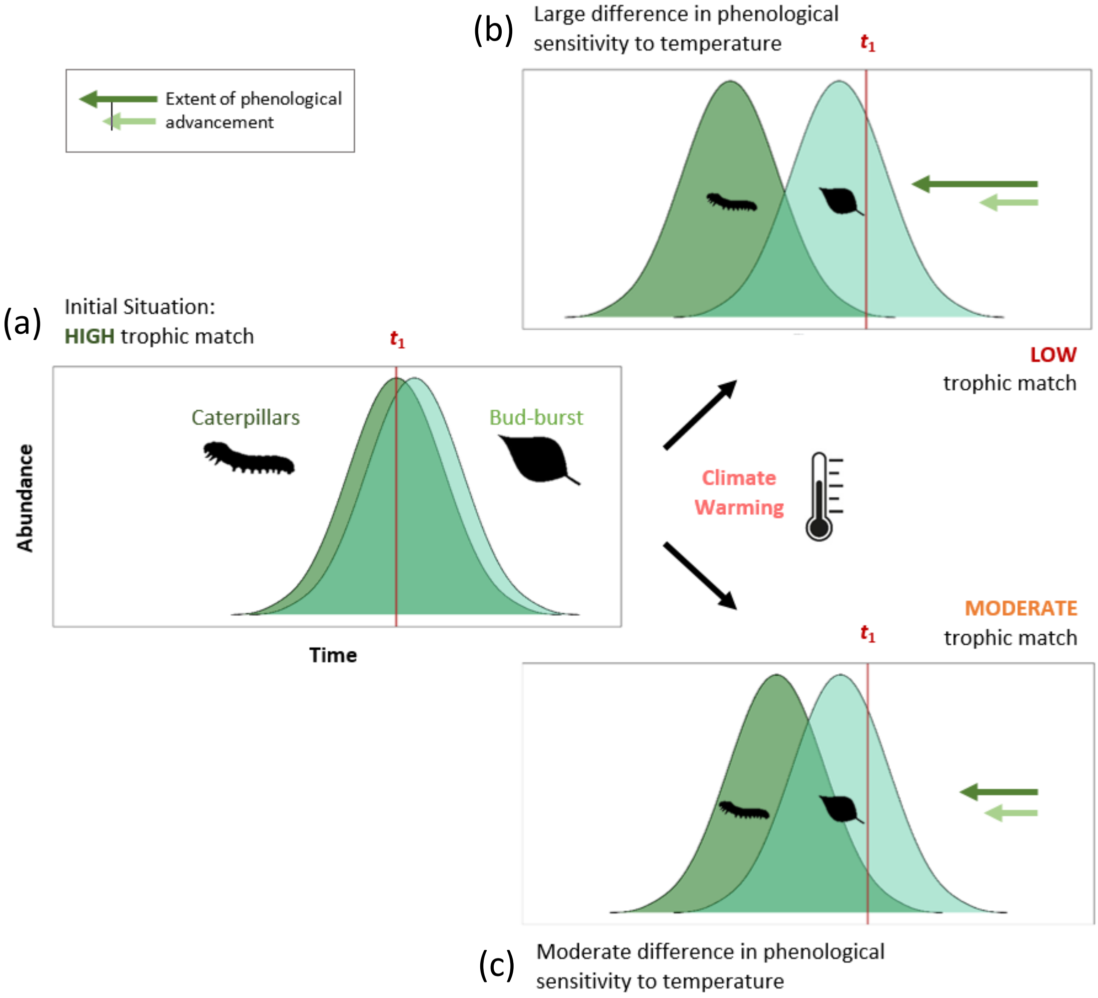

Figure 1.1. Climate warming and the match-mismatch hypothesis in spring-feeding caterpillars. When the two trophic levels are matched, the timing of caterpillar hatch mirrors closely the timing of bud-burst on their host tree in spring (a). With increasing average temperatures, both trophic levels advance their spring phenology. If one trophic level responds to a greater or lesser extent than the other (ie. if their *phenological sensitivity to temperature* is different) then mismatch will occur (b and c). The extent of this difference in phenological sensitivity to temperature can lead to more (b) or less (c) mismatch. When mismatch occurs, the phenology of the consumer is mistimed relative to its resource, and many individuals have reduced or no access to foliage to eat. As can be seen here, we could quantify mismatch either as differences in mean phenology or differences in the overlap of the two abundance-across-time curves (Ramakers *et al.*, 2020).

important, but transient, food resource for insectivorous birds nesting and rearing their chicks in spring (Gibb, 1950; Tinbergen, 1960; Perrins, 1991; Visser *et al.*, 2006; Both *et al.*, 2009; Shutt *et al.*, 2019b).

This widespread tri-trophic tree/caterpillar/bird woodland food-chain has become a standard and heavily researched model system in biology (Figure 1.2). It represents, too, a test case in which the MMH reputedly operates and in which the caveats associated with the hypothesis, outlined above, are clearly on display. Of the two studies, out of 129 analysed, that

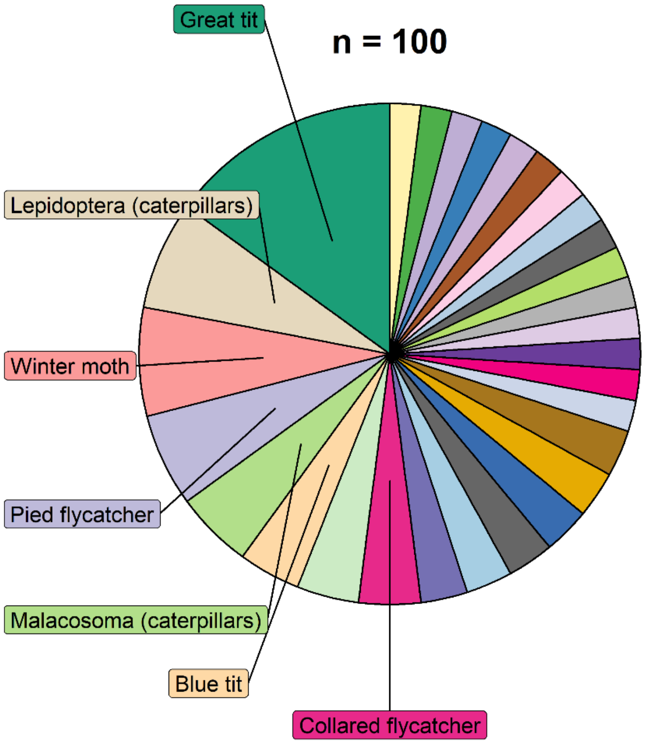

Figure 1.2. Taxonomic bias in literature on the match-mismatch hypothesis, illustrated by the relative number of studies dealing with particular species/groups. Most previous studies deal with the temperate woodland tri-trophic tree/caterpillar/bird food-chain. Particular focus has fallen upon several tit *Parus* and flycatcher *Ficedula* species as secondary consumers, and caterpillars as primary consumers, either unspecified or those of the winter moth *Operophtera brumata*. Shown here are only species and taxonomic groups which have been the subject of more than a single study. Data taken from the Supplementary material provided by Samplonius et al. (2020). See Appendix 1, Table S1.1.

Samplonius *et al.* (2020) found tested all criteria to determine whether the MMH was operating under climate change, *both* focus on woodland passerine birds and their prey, the upper two levels in this tri-trophic food-chain. In this thesis, I will use this study system to explore the extent to which natural populations might may be vulnerable to trophic mismatch induced by climate change. First, I will briefly consider climate and the MMH in the insectivorous bird component of this food chain (Section 1.3.1), before placing particular focus on the central, primary consumer link: the caterpillars (Section 1.3.2).

1.3.1. Birds and the caterpillar peak

Of those studies identified by Samplonius *et al.* (2020) as explicitly testing criteria of the MMH, three woodland bird species dominate: the great tit *Parus major*, blue tit *Parus caeruleus*, and pied flycatcher *Ficedula hypoleuca* (Figure 1.2). A great deal of our concerns, therefore, about the effects of phenological asynchrony in nature stem from studies on these three related and ecologically similar species, which presents obvious problems for extrapolating to other species more generally. Caterpillars are a particularly important component in the diet of nesting passerines (Gibb, 1950; Betts, 1955; Tinbergen, 1960; Lack, 1968, 1974; Both, 2010; Samplonius *et al.*, 2016; Verkuil *et al.*, 2022), comprising anywhere from 60 to 90% of the diet of nesting blue and great tits (Balen, 1973; Keller and Van Noordwijk, 1994; Naef-Daenzer *et al.*, 2000; Wilkin *et al.*, 2009; Both, 2010), though the precise composition of the diet can vary across the duration of chick development (Both, 2010; Samplonius *et al.*, 2016). Unlike many other insect taxa, caterpillars show a distinct peak in their temporal abundance in the diet of passerine birds (Figure 1.3) (Betts, 1955; Tinbergen, 1960; Samplonius *et al.*, 2016). Lay date and the date of peak caterpillar abundance are highly correlated across blue tits, great tits, and pied flycatchers (Both and Visser, 2005; Hinks *et al.*, 2015; Burgess *et al.*, 2018), and selection acts against late and early breeding birds, relative to this date (Perrins, 1965, 1991; Both and Visser, 2005; Samplonius *et al.*, 2016). If lay date in birds and the phenology of their prey items (peak date in caterpillars) respond differently to temperature changes of the same magnitude at this fine scale, then mismatch may arise due to climate change (e.g. Both *et al*., 2009; reviewed in Both, 2010; though for an example of differential responses to climate change leading to *increased* synchrony see Vatka *et al.*, 2011).

Global phenological trends do indeed suggest that across systems, secondary consumers tend to advance their phenology less than primary consumers in response to climate change (Thackeray *et al.*, 2016; Cohen *et al.*, 2018). Consistent with this, insects have responded more strongly than have birds (4.15 vs 2.24 days/decade) to recent increases in mean temperature (Cohen *et al.*, 2018). The caterpillar peak moves by about a month between cold and warm years (Charmantier *et al.*, 2008) and while the bird peak moves quite well to match this, by about 25 days, it does not track it perfectly (Perrins, 1965). Burgess *et al*. (2018) found that for every 10 day advance of the caterpillar peak, the three standard passerine species advanced by between 5 and 3.4 days. Across the period 1985-2000, Both *et al*. (2009) found that the date of the caterpillar peak in a Dutch population advanced significantly more than bird breeding phenology. Perrins (1991) found selection was stronger against breeding later in birds than against breeding earlier (Selection differential approx. -0.5 vs 3.0 at 6 days early

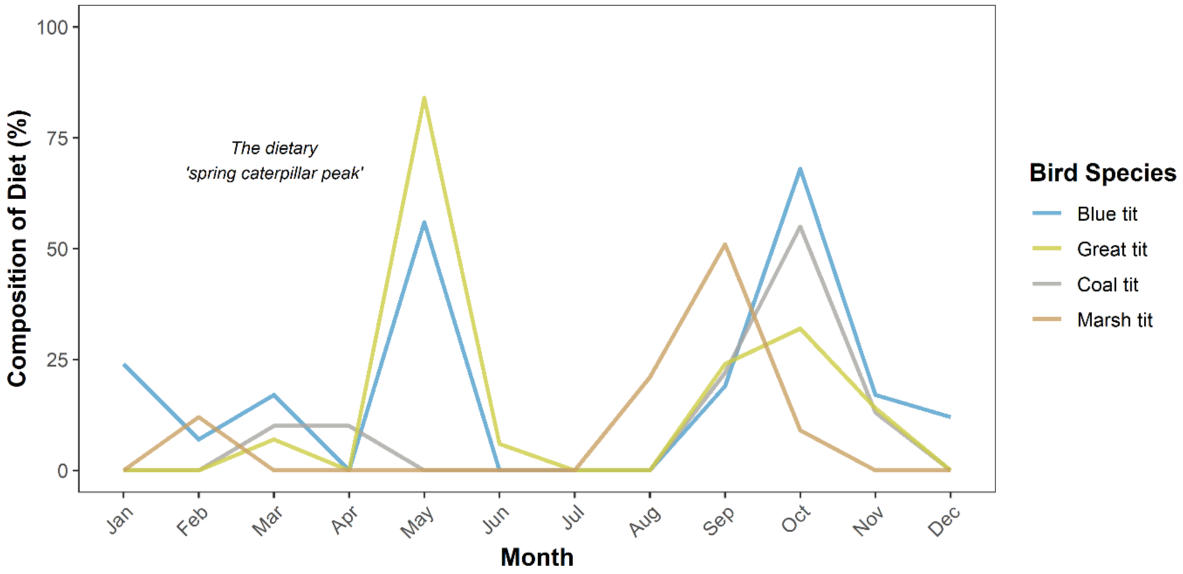

Figure 1.3. Changes in the importance of caterpillars in the diet of tit *Parus* species across the year, at the Forest of Dean, Gloucestershire (Great Britain). There are consistent and often cross-species temporal trends in the importance of caterpillars as a prey item. In early spring, as birds are breeding, caterpillars rapidly come to comprise a substantial majority of prey items, coinciding with a sudden increase in their abundance in the field as trees come into leaf. Data taken from Betts (1955). See Appendix 1, Table S1.2.

vs late). Consistent with these findings, Both and Visser (2001) estimated that selection for early breeding between 1980 and 2000 was increasing in pied flycatchers.

However, the phenological changes observed in passerine populations across time presents a complex picture (Both, 2010). At sites in the Netherlands and the United Kingdom, for example, despite equivalent advancement in the timing of the caterpillar peak (Charmantier et al., 2008; Both, 2010), we find different degrees of advancement in great tit lay date: in some populations synchrony *decreases* (Visser *et al.*, 1998; Both *et al.*, 2009), while in others it has been observed to *increase* over time (Cresswell and McCleery, 2003; Charmantier *et al.*, 2008). Similarly, we find that changes in relative synchrony between pied flycatchers and the caterpillar peak is highly contingent on the particular geographical population involved (Both and Visser, 2001, 2005; Sanz *et al.*, 2003; Ahola *et al.*, 2004; Both *et al.*, 2009; Thackeray *et al.*, 2016). For these species, then, that have perhaps been subject to more detailed study in relation to the MMH than any others (Figure 1.2), we find strong support for the idea that synchrony with the ephemerally abundant spring caterpillars is indeed important for fitness (Criteria 1 and 4), and that the extent of that synchrony can be driven by between-year variation in temperature (Criterion 3). Phenological trends across time among populations are less consistent (Criterion 2), as are the effects of synchrony on population-level fitness, size, and persistence (Criterion 5). The effects of climate change on the occurrence of mismatch in these populations, and the ultimate effects of that asynchrony, seem to be highly contingent on geographical location, associated ecological interactions, and the particular species involved—the ubiquity of any negative effects due to temperature induced mismatch, and their severity, is therefore far from clear.

1.3.2. Caterpillars and the flush of spring foliage

As the central component of the tree/caterpillar/bird woodland food-chain, caterpillars are key—the dynamics of their populations have the potential to affect species at both higher and lower trophic levels (Marquis and Koptur, 2022). Their abundance will mediate not only the availability of food resources for nesting birds (see Section 1.3.1) but also, for example, the extent of feeding damage to which the young foliage of trees is subjected (Feeny, 1970; Tikkanen *et al.*, 1998; Kulman, 2003; Wesołowski and Rowiński, 2006, 2008; van Asch and Visser, 2007; Rieske and Dillaway, 2008; Simmons *et al.*, 2014; Visakorpi *et al.*, 2020; Sarvašová *et al.*, 2021). Predators exerting top down pressure on caterpillar population size can indirectly affect the growth and development of the host-plants they feed on (Whittaker and Warrington, 1985; Marquis and Whelan, 1994). Despite their crucial importance as consumers and as prey, however, the phenological strategies and the response of phenology to climate change of this central group in woodland food-webs has received comparatively little attention in the literature, compared with higher trophic levels (Figure 1.2.) (Samplonius *et al.*, 2020).

The appearance of foliage on trees in spring is spatially and temporally heterogeneous (Hinks *et al.*, 2015), depending on local weather conditions and microclimate, especially temperature, which can differ across a range of spatial scales and between years. In addition, leafing phenology can differ between tree species, as do plastic responses to different environmental conditions (Lechowicz, 1984; Crawley and Akhteruzzaman, 1988; Kramer, 1995; Ducousso *et al.*, 1996; Wielgolaski, 2001; Karlsen *et al.*, 2007; Wesołowski and Rowiński, 2008; Willis *et al.*, 2008; Vitasse *et al.*, 2009; Polgar and Primack, 2011; Basler and Körner, 2012; Panchen *et al.*, 2014; Schuster *et al.*, 2014; Wolkovich *et al.*, 2014; Marchin *et al.*, 2015; Lenz *et al.*, 2016; Cole and Sheldon, 2017; Denéchère *et al.*, 2018; Geng *et al.*, 2020). For caterpillars, and other phyto- and foliophagous spring insects, their survival and fitness depends to a substantial degree on matching the timing of their appearance with the timing of the appearance of this new foliage (e.g. Southwood *et al*., 2004). The sudden flushing of fresh foliage on trees represents a fleeting and abundant new resource which they can exploit, if they time their phenology correctly.

Lepidoptera (butterflies and moths) can pass the winter in almost all their life history stages, though there seems to be tendency for some stages to be used rather than others (Young, 1997). Where caterpillars commence feeding early in spring, individuals typically pass the previous winter season as a diapausing caterpillar or an egg (Leather *et al.*, 1993). The increase in spring temperatures serves to induce a break from larval diapause (Leather *et al.*, 1993) or hatching from eggs, as in the winter moth *Operophtera brumata* (Figure 1.4) (Speyer, 1938; Embree, 1970; Watt and McFarlane, 1991; Buse and Good, 1996; Visser and Holleman, 2001; Tikkanen and Lyytikäinen-Saarenmaa, 2002; van Asch *et al.*, 2007, 2012; Hibbard, 2014; Hibbard and Elkinton, 2015; Salis *et al.*, 2016). Caterpillars which hatch or break diapause too early, before buds have burst and leaves have begun to appear on their host trees, find themselves without food and starve, either dying or suffering reduced fitness later in life (Cuming, 1961; Wint, 1983; Tikkanen and Julkunen-Tiitto, 2003). Caterpillars which hatch too late are forced to feed on increasingly mature foliage, which becomes tougher and accumulates increasing quantities of noxious secondary chemicals such as tannins, making it less palatable than younger leaves (Feeny, 1968, 1970; Tikkanen and Julkunen-Tiitto, 2003). Selection therefore seems to act to promote the close synchrony of caterpillar and host-plant phenology in spring (Tikkanen and Julkunen-Tiitto, 2003; van Asch *et al.*, 2007), such that we see in caterpillars a distinct peak of abundance in early spring (e.g. Holliday, 1977). The ‘caterpillar peak’ contrasts with other groups of insects which do not show the same marked and ephemeral changes in their availability (e.g. Dunn *et al.*, 2011).

The degree of synchrony between the caterpillars and their host-plants, and the inferred degree of match or mismatch, seems to be a key, perhaps paramount, factor in determining the between-year fluctuations in their population sizes (Varley *et al.*, 1974). As in the case of their bird predators, the degree of caterpillar mismatch with their host-plants, in the context of recent climate warming, depends on the extent to which the timing of the caterpillar peak and the timing of host bud-burst respond *differently* to *the same temperature stimulus*. The

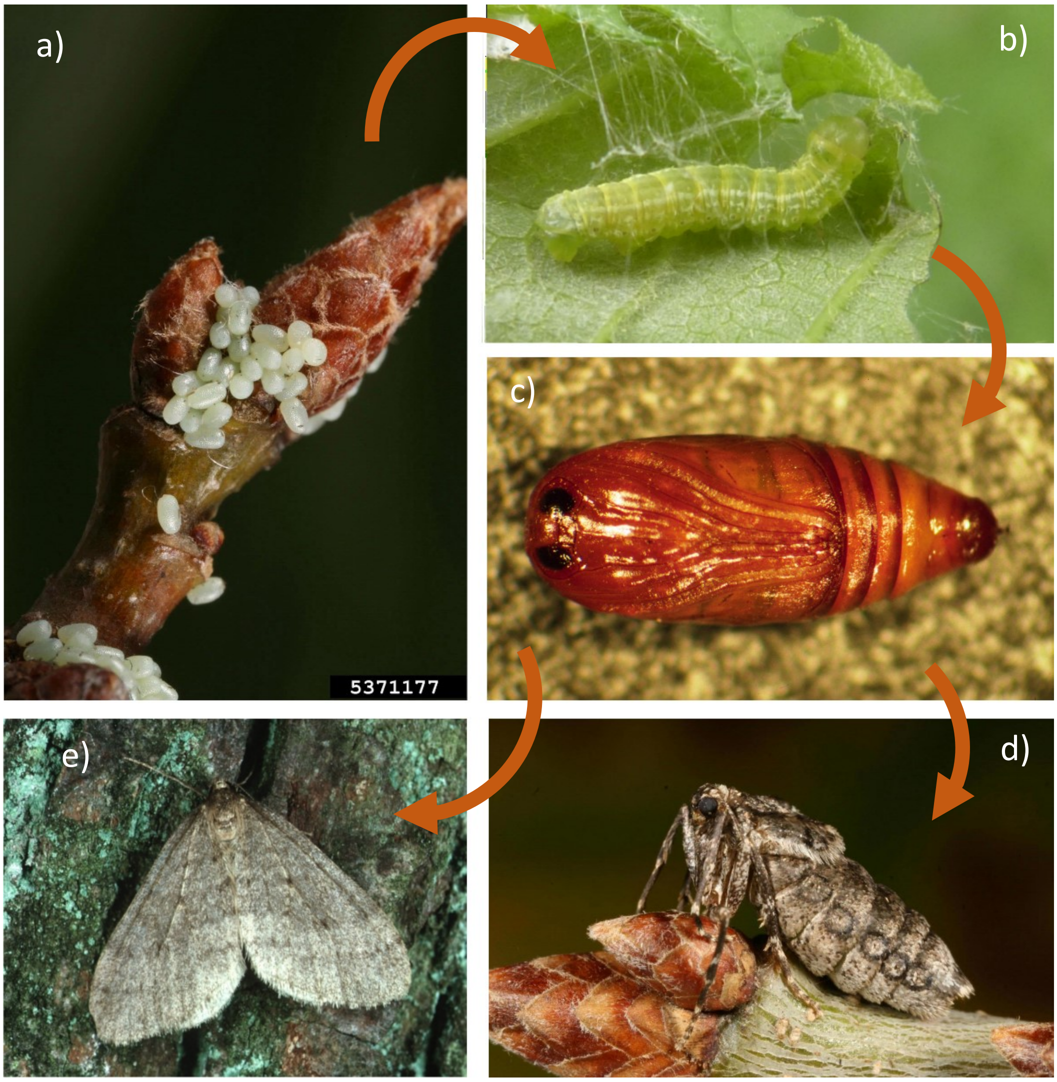

Figure 1.4. The life cycle of the winter moth *Operophtera brumata.* (a) Eggs are laid by wingless females during the winter months. (b) These hatch as buds begin to break on trees in early spring, and caterpillars feed over the subsequent weeks, taking typically 20-30 days to reach pupation. (c) Caterpillars descend from the tree and pupate in a loose spinning among leaf litter and soil. In mid-winter, (d) wingless adult females and (e) fully winged males eclose. (d) Females ascend a nearby tree to lay their eggs in upper branches and the canopy, mating en route. Image credits: a) Gyorgy Csoka, Hungary Forest Research Institute; b) Graham Calow; c) Hannes Lemme; d) Gyorgy Csoka, Hungary Forest Research Institute; e) Louis-Michel Nageleisen, Département de la Santé des Forêts. From ForestPests.org, reproduced under a CY BY 3.0 licence.

date of the caterpillar peak is highly correlated with the bud-burst date of their host trees (Buse *et al.*, 1999; Both *et al.*, 2009; Cole *et al.*, 2015; Hinks *et al.*, 2015; Burgess *et al.*, 2018). At a Dutch site, Both *et al.* (2009) found a significant correlation between the caterpillar peak and bud-burst on oak (1 day delay in oak bud-burst delayed the caterpillar peak by 0.75 days [SE 0.18]), and a slope which did not deviate significantly from direct proportionality in the period 1985-2005, implying that caterpillar phenology was exactly tracking that of their host-plants. As expected given this, the degree of asynchrony between the two did not change over that time frame as a result of increasing spring temperatures (Both *et al.*, 2009). However, caterpillars tend to respond to increasing temperatures by advancing their phenology to a greater degree than their host trees, by 0.75 days/year (see also Visser *et al*. [2006], who estimated this at 0.74 days/year) for the caterpillars versus 0.17 days/year (Both *et al.*, 2009) for the trees[1]. At Wytham Woods, in Oxford, a similarly strong correlation between caterpillar and tree phenology has been found (r = 0.69 CIs: 0.295 to 0.963). Although displaying a slight tendency towards exceeding unity (ie. caterpillars advancing their phenology to a greater degree than their hosts) this deviation is again not significant (1.788 CIs: 0.497 to 3.896) (Burgess *et al.*, 2018). Interestingly, and in contrast to these studies, Charmantier *et al*. (2008) found a parabolic trend in caterpillar peak date—using a dataset which began slightly earlier (from 1961-2007)—which reached its latest around 1980, after which peak date has been advancing. Further, a Polish study found that while peak date varied significantly across years, it showed no clear trend across two wooded sites (Nadolski *et al.*, 2021). Patterns of shifts in peak date are therefore not consistent across populations.

Generally speaking, the caterpillar peak occurs earlier in warmer years (Visser *et al.*, 1998, 2006; Charmantier *et al.*, 2008; Macphie *et al.*, 2022), and has been advancing across recent decades (Visser *et al.*, 1998, 2006; Both *et al.*, 2009; Vatka *et al.*, 2011). At sites across Scotland, Macphie *et al*. (2022) found that the peak advanced by 4.96 days/°C [CIs: 6.21, 3.64]. In contrast to the rather different *temporal* changes that have been recorded in the timing of the caterpillar peak versus plant phenology in natural populations, the mean phenological

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[1] Notably, this trend in the caterpillar peak is also significantly greater than that of their passerine predators, which advanced, in aggregate, by about half as much (Both *et al.*, 2009)—similar to the relative difference estimated by Burgess *et al*. (2018) . This is qualitatively consistent with the general findings of Thackeray *et al.* (2016), that primary consumers respond most strongly to spring warming. Equally, considering primary producers, Menzel *et al*. (2006) find a mean advancement of plant spring phenology of 2.5 days/decade, and Parmesan (2007) estimate plant phenological events as advancing 1.1-3.3 days/decade.

sensitivity to temperature is rather similar between these two groups—in plants: 4.6 days/°C (Menzel *et al.*, 2006), 5 days/°C (Amano *et al.*, 2010), 4.3 days/°C (Thackeray *et al.*, 2016), 4-9 days/°C (Wolkovich *et al.*, 2012), 5-6 days/°C (Karlsen *et al.*, 2007). The evidence that other environmental or geographical factors affect the timing of the caterpillar peak, perhaps mediated by temperature, is conflicting. In Britain, for example, the date of the caterpillar peak is delayed with increasing altitude (1.3 days/degree N. [Burgess *et al.*, 2018]) and elevation (3.7 days/100m [Shutt *et al.*, 2019]). In contrast, Schöll *et al*. (2016) asserted that across several populations in Austria altitude had no effect, though this study likely lacks the power to support such a claim (Macphie *et al.*, 2022).

Although the mean or median of the caterpillar peak—the point at which the maximum abundance or biomass of caterpillars is measured or inferred—has been historically the primary focus of research, Cushing (1982)[2] himself, in early work on the MMH, made it clear that other attributes of the shape or conformation of the resource peak could modulate the effects of asynchrony. As well as shifts in mean or median date, the height, width, and duration (linked, but not identical, to width) can vary across space and time (Visser *et al.*, 2006; Smith *et al.*, 2011; Shutt *et al.*, 2019a; Macphie *et al.*, 2020, 2022). At higher elevations, peaks can be higher but more peaked, relative to lower but less severely declining peaks at lower altitudes (Shutt *et al.*, 2019a). In warmer springs, the peak is earlier, higher, and narrower (Macphie *et al.*, 2022), consistent with the theoretical expectations of a growing degree day model of caterpillar growth and development (that is to say, where growth is dependent on temperature, growth will accumulate more swiftly in warmer years, e.g. Hibbard and Elkinton, 2015; Salis *et al*., 2016). Although there is a great deal of variation, peak caterpillar abundance may increase by a third in warmer years (Macphie *et al.*, 2022)—this relationship with temperature could be quadratic, however, such that very high temperatures once again yield broader peaks (Smith *et al.*, 2011), perhaps due to favourable conditions leading to increases in overall caterpillar abundance (effectively, the area under the caterpillar peak increases in size), though the evidence is not clear (Macphie *et al.*, 2022).

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[2] "The production of fish larvae in time should be matched or mismatched to that of their food. If matched, recruitment would be high within the limits of variation of the primary production. If mismatched, recruitment will be low—more so if primary production is low, but less so if it is high" (Cushing, 1982).

There is some limited evidence which hints that in warmer years, overall caterpillar biomass does increase (Visser *et al.*, 2006; Macphie *et al.*, 2022).

Temperature driven changes in the timing and shape of the caterpillar peak are not necessarily equal across space and time, nor is the peak itself a universal phenomenon in all temperate arboreal caterpillar populations. In nature, while the concept of a “peak” frequently describes temporal and seasonal variation in caterpillar abundance, that is not always the case. In several beech-dominated Austrian woodlands, for example, Schöll *et al.* (2016) found extremely variable caterpillar abundance, across sites, and variation between individual trees. Burger *et al*. (2013) found that in contrast to a Dutch site (principally oak), where spring-time caterpillar abundance showed a classic peaked pattern, at a Swedish site (pine, birch, with some few oaks) there was fairly low and constant caterpillar abundance throughout the season, with no clear peak. Indeed, the relative abundance of different host-plant species and the density of host trees within a site can exert a significant effect on both the timing and shape of the caterpillar peak, perhaps even to the level of individual trees (Sarvašová *et al.*, 2021). There is therefore variation in the caterpillar peak across a range of spatial scales, across time, across habitat types, and geographical locations, and our knowledge of these patterns and our understanding of the mechanisms driving them is very incomplete. This variation makes it difficult to make robust general claims as to the extent to which climate change could drive mismatch between these taxa and their host-plants.

1.4. Difficulties for the theory: caterpillars and the simplification of a complex system

In the context of the MMH, the tree/caterpillar link of the tree/caterpillar/bird food-chain has received comparatively far less attention (Figure 1.2). Where the caterpillars—the central component of these trophic systems—have been the subject of investigation, this is almost always as a homogenous “caterpillar peak”—as a food resource for higher trophic levels. In fact, the picture is far more nuanced than this, and, as yet, our appreciation of the importance of these subtleties in the dynamics of the MMH is in a very under-developed state.

The conventional story of mismatch in arboreal caterpillars can be summarised, briefly, as follows:

1) Bud-burst occurs on deciduous trees during a narrow time window in spring
2) In spring-feeding caterpillars, fitness declines very rapidly for individuals hatching too late or too early, with respect to host tree bud-burst phenology
3) If caterpillar and tree phenology respond differently to climate warming, by advancing to different degrees, mismatch will occur, with fitness implications for both taxa (see Figure 1.1)

A closer examination of the literature and some consideration of the ecology of these species clearly shows that, at the very least, each of the precepts are severe simplifications, if not false. Next, I will briefly consider a number of significant caveats to this standard story of woodland caterpillar mismatch. These simplifications highlight the superficiality with which we have, in my view, hitherto attempted to understand how this system operates in nature, and from which we have attempted to make predictions of future change.

1.4.1. There are many spring-feeding caterpillar species

A majority of the literature on mismatch and the caterpillar peak focuses on one particular caterpillar species, the winter moth *Operophtera brumata* (van Asch and Visser, 2007) (Figure 1.4). There are some exceptions, and this frequently depends on the methods used to quantify caterpillar abundance across time in the environment (Zandt, 1994). Older studies often attempt to measure this directly, through a combination of: twig sampling, where foliage in a fixed area is either searched *in situ* or clipped and searched in the lab (Tinbergen, 1960); and, monitoring larval "half-fall"[3], a technique involving the use of water traps which catch and kill caterpillars descending from the tree canopy when fully grown to pupate in leaf litter (Perrins, 1965; Charmantier *et al.*, 2008; Cole *et al.*, 2015, 2021; Hinks *et al.*, 2015). An alternative approach which is more often utilised is to place large nets or cones beneath the canopy of trees to record "frass-fall", the quantity of excrement pellets (called "frass") produced by caterpillars falling to the ground. This is visually recognisable and the quantity and size of the frass collected can be used as a proxy for caterpillar abundance (Tinbergen, 1960; Balen, 1973; Visser *et al.*, 1998, 2006, 2021; Wesołowski and Rowiński, 2006, 2008;

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[3] Specifically, this refers to the point at which 50% of all the caterpillars which are recorded via this method have descended to pupate, hence "half-fall".

Smith *et al.*, 2011; Vatka *et al.*, 2011; Samplonius *et al.*, 2016; Burgess *et al.*, 2018; Nadolski *et al.*, 2021). However, it is not possible to discriminate morphologically between the frass of different caterpillar species and, as such, studies using frass-fall aggregate the abundance of all caterpillar species. Although frass-fall correlates very well with caterpillar density at the canopy level (Tinbergen, 1960), environmental conditions changing the feeding rate might modulate the strength of this relationship (Tinbergen, 1960; Tinbergen and Dietz, 1994), and there is therefore a problem with drawing direct comparisons between studies using half-fall and frass-fall data. Finally, a small number of studies have attempted to use branch beating to directly sample caterpillars from foliage (Shutt, 2017; Shutt *et al.*, 2019a; Macphie *et al.*, 2020, 2022) which allows discrimination between species and direct measurement of changes in both abundance and biomass across time, but presents its own methodological problems (Shutt *et al.*, 2019a)—for example, some parts of a tree are more accessible than others (e.g. the lower boughs), and if within-tree caterpillar dispersal is very restricted, repeated measurements of these parts might obtain skewed results.

Caterpillars comprising the spring-feeding arboreal guild are taxonomically disparate (Smith *et al.*, 2011; Kulfan *et al.*, 2018; Shutt *et al.*, 2019a), and often differ a great deal in other aspects of their life history and biology (van Asch and Visser, 2007; Porter, 2010; Henwood *et al.*, 2020). However, where discrimination is possible between species, these other species have often been ignored and the winter moth, a small Palaearctic geometrid, is taken as either the most important species, or representative of the entire guild—it has become the standard caterpillar study species in this system (Varley *et al.*, 1974; van Asch and Visser, 2007). Although the winter moth is indeed often the dominant species of the spring caterpillar peak, in terms of both biomass and numerical abundance, other species still occur, and often at significant levels (Feeny, 1970; Kulfan *et al.*, 2018; Shutt *et al.*, 2019a). In a series of sites systematically sampled across Scotland, winter moth made up approximately one third of all individuals (Shutt *et al.*, 2019a). Both experimental and observational work in the field seeking to understand the synchrony between spring caterpillars and their hosts and predators, and how this will change in future, almost always focuses on the winter moth (van Asch and Visser, 2007; see also Chapter 3).

This limited perspective is significant when we consider climate warming in spring, and the MMH. There is no reason to assume that the phenological sensitivity to temperature—and hence the extent of any asynchrony or mismatch experienced with the host-plant—will be equal across all caterpillar species. Indeed, the evidence for this is limited and mixed (e.g. Sarfraz *et al.*, 2013; Schwartzberg *et al.*, 2014; Despland, 2017). Differential phenological sensitivity across caterpillar taxa has the potential to reduce the overall level of mismatch experienced between each of the neighbouring trophic levels. Rather than the caterpillar peak advancing as a single entity, different responses by the different species comprising it might alter its shape, flattening the peak out, providing a buffer to species relying on the caterpillars as food, or perhaps making available new caterpillar species as prey which previously occurred too early or late to be utilised.

1.4.2. Spring caterpillars exploit a wide range of host-plant species

As well as focusing almost exclusively on the winter moth, there is an almost exclusive focus on oak, particularly English oak *Quercus robur*, as a host-plant in the phenological literature. This is despite the fact that the winter moth is one of the most polyphagous British moth species, having been recorded feeding on 31 different genera across 15 families, on species as disparate as birch, heather, and bilberry (Robinson *et al.*, 2010). Despite being largely ignored or given only passing reference in the phenological literature, the broad diet of this species has long been known and acknowledged, particularly in the entomological literature (Stainton, 1859; Meyrick, 1895; Stokoe, 1948a; Skinner, 2009; Porter, 2010; Waring *et al.*, 2017; Henwood *et al.*, 2020). Many other members of the spring feeding caterpillar guild are also highly polyphagous (Porter, 2010; Henwood *et al.*, 2020). The relative importance of these different host-plants to the winter moth and to other caterpillar species, in terms of larval fitness and performance, and how this varies across different populations remains unclear.

The relative and absolute phenology of each of these different tree taxa, the processes of plant growth, leaf maturation (both structural and biochemical), and the extent of their phenological response to warming spring temperatures, is likely to differ across species (Feeny, 1968, 1970, 1976; Lechowicz, 1984; Schroeder, 1986; Crawley and Akhteruzzaman, 1988; Hunter, 1991; Kramer, 1995; Ducousso *et al.*, 1996; Myneni *et al.*, 1997; Williams *et al.*, 1998; Wielgolaski, 2001; Haukioja *et al.*, 2002; Tikkanen and Julkunen-Tiitto, 2003; Menzel *et* *al.*, 2006; Karlsen *et al.*, 2007; Wesołowski and Rowiński, 2008; Willis *et al.*, 2008; Vitasse *et al.*, 2009; Polgar and Primack, 2011; Basler and Körner, 2012; Panchen *et al.*, 2014; Schuster *et al.*, 2014; Wolkovich *et al.*, 2014; Marchin *et al.*, 2015; Lenz *et al.*, 2016; Thackeray *et al.*, 2016; Cole and Sheldon, 2017; Cohen *et al.*, 2018; Denéchère *et al.*, 2018; Geng *et al.*, 2020; Roslin *et al.*, 2021; Gaytán *et al.*, 2022). Further complicating the picture, different caterpillar species have different host-plant preferences (Maitland Emmet and Heath, 1992; Skinner, 2009; Porter, 2010; Henwood *et al.*, 2020). All of these factors could conceivably combine to create a far more complex pattern of resource availability in spring for the caterpillars, both as an underlying baseline and also under changing climatic conditions. The degree of variation which exists across host-plant species might mean the 'spring peak' of availability of especially palatable foliage is broader, less distinct, and spread across a more protracted time scale. This might entail less severe fitness effects of mistiming than has previously been thought. As yet, however, we simply have insufficient information to judge if, and to what extent, this might be the case, and how caterpillars, and other similar species, might be "buffered" against mismatch induced by climate warming.

1.4.3. Environmental conditions and individual phenology both vary

Making the simple claim that increasing spring temperatures could shift caterpillar phenology out of alignment with that of their hosts ignores the often dramatic variation present in the phenology of both trophic levels, often across a very small spatial scale. Individual host trees and caterpillars show significant variability in their phenology due to genotypic differences and phenotypic plasticity under different environmental conditions. Even when kept under constant conditions, for example, there is considerable variation in hatch date within winter moth broods—the offspring of a single female moth (Speyer, 1938; Watt and McFarlane, 1991; Kerslake and Hartley, 1997; Tikkanen and Lyytikäinen-Saarenmaa, 2002; Tikkanen and Julkunen-Tiitto, 2003). This arises from genetic differences in the reaction norms of the response of phenology to temperature (van Asch and Visser, 2007; van Asch *et al.*, 2007, 2012). Individual trees, across a range of different species, can vary dramatically in their phenology—even individuals of the same species in very close proximity to one another in the field can be at very different phenological stages, progressing at different rates (e.g. Figure 1.5, from Wesołowski and Rowiński [2008]).

Figure 1.5. The scale of phenological variation in trees. Two oaks *Quercus robur* growing immediately beside one another showing dramatic differences in leafing phenology. The fate of a caterpillar hatching out in spring could depend on which side its mother chanced to ascend during the winter months. Reproduced from Wesołowski and Rowiński (2008).

In addition to intrinsic genetic differences in the response to environmental conditions, those conditions themselves can vary, across a range of spatial scales—winter moth eggs on the north- and south-facing side of a single tree, for example, can hatch several days apart, depending on weather conditions (Hibbard and Elkinton, 2015). Different parts of the same trees can show significantly different phenology—sycamore, for example, is particularly notable in frequently having the lower leaves well advanced in growth and development, while buds at the top of the canopy, being more exposed to weather conditions, have barely opened (see Figure 6.5). Match and mismatch in this system is usually conceptualised at the level of a whole site, comprising many individual trees and moth broods. Such a coarse-grained level of analysis could easily obscure fine-grained match and mismatch, occurring at a very small spatial scale within the broader site, regardless of the overall average phenology of each trophic level. Rather than a simple pair of consumer and resource peaks, which shift under changing conditions (Figure 1.1), there may be many such peaks, across individual patches of woodland, trees, and within individual trees. This great degree of variation may reduce the extent of mismatch under climate warming, at small spatial scales.

1.4.4. Caterpillars inhabit a complex spatial environment of host-plants

Not only do caterpillars experience significant variation in abiotic conditions, such as temperature, across very small spatial scales—causing commensurate variation in their phenology across these scales—they also face considerable variation in their biotic environment. Assuming that a fairly steep peak of optimum palatability exists during which they must exploit their host-plants (Tikkanen and Julkunen-Tiitto, 2003; van Asch *et al.*, 2007), any individual caterpillar is likely to find itself faced with greatly variable probabilities of survival simply by dint of the spatial location it happens to find itself in. As Cole *et al.* (2015) have pointed out, the scale at which these organisms experience the environment is a crucial, and often neglected, aspect of the MMH in this system. From the perspective of a neonate winter moth caterpillar, for example, a woodland in spring is a mosaic of patches of foliage and unopened buds, each varying in their underlying (i.e. specific or individual) and age-related palatability. Tikkanen and Julkunen-Tiitto (2003) found that certain individual trees within a site were unsuitable for caterpillars because they matured more rapidly. Female winter moths seem to exercise limited (if any) choice in the individual host-plants on which they lay (Connell, 2013) (Figure 1.4), although they may spread their ova around on a given individual, and seem unable to predict the environment their offspring will find themselves in when spring arrives. This, alongside the unpredictability in the phenological environment at the level of individual parts of the same tree, between tree individuals, and across microhabitats within a woodland side, might serve to promote variation in the phenology of caterpillars, such that, in nature, we would see a broad, gradually declining pulse, rather than a steep peak, of caterpillars hatching across time (some studies, using frass-fall as a proxy, have noted this, to varying degrees across populations, e.g. Tinbergen, 1960; Burger *et al.*, 2013; Schöll *et al.*, 2016; Shutt et al., 2019). The nature of such an effect would vary, depending on the degree to which a woodland, viewed from a caterpillar's perspective, was heterogeneous. Environmental heterogeneity of this kind, alongside a narrow focus on oak as the main host-plant species, might explain something of the conflict evident between different studies, some of which suggest *increasing* asynchrony between caterpillars and their hosts with increasing spring temperatures (Visser and Holleman, 2001; Burgess *et al.*, 2018) and others which do not (Buse *et al.*, 1999; Both *et al.*, 2009). Indeed, this fact may lead us to question whether or not synchrony is actually the baseline condition in this system at all (Singer and Parmesan, 2010)—that is to say, an individual caterpillar might be asynchronous (and suffer mismatch) with an individual host tree but, stepping back to the population level, mean caterpillar fitness might be maximised when averaged across that population. The average caterpillar phenology at a site may be adapted to the average host-plant phenology of that site, adjusted for the inherent palatability of each host species. The patchy, phenologically heterogeneous nature of the environment in which arboreal caterpillars find themselves could feasibly serve to dampen the effects of asynchrony with any one particular host tree, particularly since those trees themselves might respond differently to spring warming. In the context of climate change, this heterogeneity could provide a further buffer against mismatch at the population level.

1.4.5. Caterpillars possess adaptations to reduce the negative fitness effects of asynchrony

The fitness costs of hatching early or late in spring for a caterpillar are likely not symmetrical (Tikkanen and Julkunen-Tiitto, 2003): hatch too early, before food is available, and caterpillars will starve in a fairly short time; hatch too late, however, and foliage is more widely available for the caterpillars to feed on, but is progressively (perhaps precipitously) deteriorating in palatability. Late hatching caterpillars therefore suffer reduced fitness on average, but those consequences are not so severe compared with early hatching. On the face of it, the conservative strategy would seem to be to hatch consistently late. However, caterpillars can employ behavioural and physiological mechanisms to minimise some of the deleterious effects associated with early hatching (Despland, 2017). In the winter moth, the ability of neonate caterpillars to tolerate periods of starvation and wait until buds begin to break and foliage appears may increase their survival (Kozhanchikov, 1950; Cuming, 1961; Wint, 1983; Tikkanen and Julkunen-Tiitto, 2003), although enduring starvation may impact individual fitness later in life (Wint, 1983).

Furthermore, if caterpillars find themselves in an area with no available food they can disperse via ‘ballooning’—young first or even second instar individuals spin a length of silken thread which catches the wind, carrying the caterpillar off to a new location (Briggs, 1957; Embree, 1965; Edland, 1971; Capinera and Barbosa, 1976; Holliday, 1977; Wint, 1983; Johns and Eveleigh, 2013; Despland, 2017). Such a strategy is, of course, extremely risky, and it is highly unlikely to yield successful results, but could improve an individual’s chance of survival in a very dire situation. Indeed, the propensity to balloon seems to increase with increasing starvation (Tikkanen and Lyytikäinen-Saarenmaa, 2002). This behaviour could even be used in a case of extreme late hatching, where all foliage was past the point of acceptability (Pepi *et al.*, 2016).

The foregoing discussion accepts that caterpillars which hatch too early cannot exploit the trees around them *before* bud-burst. This is a point frequently emphasised in the phenological literature (see Table 4.1). However, earlier entomologists, beginning in the late nineteenth century, concerned primarily with documenting the biology of these species, made frequent reference to individual caterpillars burrowing into unopened or barely expanded buds, to eat the fresh, unexposed foliage within (Stokoe, 1948a). Such behaviour would allow caterpillars to sustain themselves, at least for a time, despite hatching asynchronously with the date of true bud-burst on their hosts. A combination of these three mechanisms—starvation tolerance, ballooning, and bud feeding—might act concurrently to ameliorate the deleterious effects of early and late hatching, meaning that caterpillar fitness may not decline as steeply as is typically assumed with increasing asynchrony.

1.5. Thesis Aims

I have attempted here to describe the theoretical background to the match-mismatch hypothesis, its broad-scale application across trophic levels, and have considered, in depth, the particular case of the tree/caterpillar/bird food-chain, which has become one of the standard study systems in which the hypothesis is conceptualised and tested. I have been at pains to emphasise what I consider to be the deficiencies or weaknesses in our current understanding of the MMH in this woodland food-chain, and in particular the far less well understood tree/caterpillar link in that chain. Quite at odds with the standard story of the MMH, there are a number of ways in which the effects of mismatch might be ameliorated in this system, and perhaps more widely. Such mechanisms are therefore very significant with regard to the effects of any future climate change but also, more fundamentally, as insights into how these interactions have arisen and how they are maintained.

The aim of this thesis is to address several of the caveats to the standard story of mismatch in the tree/caterpillar food-chain, as outlined above. In:

- Chapter 2, I will consider the relative significance of a range of tree species as host-plants for the winter moth, moving beyond the narrow focus on oak, particularly English oak *Quercus robur*. I quantify fitness across host-plant species and consider how this varies between different geographical populations.
- Chapter 3, I will consider the effects of late hatching asynchrony on fitness across a range of spring-feeding caterpillar species, feeding on a taxonomically diverse range of common host-plant species. In so doing, I hope to advance our understanding of the ubiquity of any deleterious effects of asynchrony across both different host-plants species and different caterpillar species, moving beyond the grossly simplified winter moth/oak system.
- Chapter 4, I will address mechanisms allowing caterpillars to cope with early hatching. I will examine the extent of their ability to tolerate various degrees of starvation across a range of different spring-feeding caterpillar species. In addition, I experimentally test the degree to which winter moth caterpillars can utilise the unopened and developing buds of various host-plant species.
- Chapter 5, using a similar approach to frequently cited, classic literature, I will examine how winter moth caterpillar growth rates differ across host-plant species and degrees of late-hatching asynchrony. I will determine the extent of variation in these responses between caterpillar broods and between individual trees, and consider how such phenological variation across a population might act as a factor ameliorating any deleterious effects of asynchrony.
- Chapter 6, drawing on the work of the previous chapters, I will attempt to define and develop the concept of *buffering*—a term widely used in the literature, but which has hitherto received little explicit consideration as a theoretical principle. I will consider the extent to which buffering against inherently unpredictable or variable environmental conditions might in turn ameliorate the impacts of future climate change, focusing on phenological mismatch in the spring-feeding caterpillar system as a test case.

To do so, I employed a large-scale experimental approach, rearing caterpillars in captivity using ova obtained from females collected regularly each winter in the field. I developed a rearing protocol for caterpillars, and a method for efficiently collecting and recording female winter moths in the field (see Appendix 9). The use of experiments contrasts with much of the work on this system, which focuses on observational studies in the field, and I believe the comparison between these different approaches can offer us fresh insights into the mechanisms governing the interactions between these species.

Chapter 2: Polyphagy in the winter moth and its role in buffering phenological mismatch

2.1. Abstract

Climate change may disrupt phenological synchrony between interacting species with different phenological sensitivities to temperature. Potential trophic mismatch between the winter moth *Operophtera brumata*, an abundant temperate spring-feeding species, and oak, one of the host-plants of its caterpillars, as a result of climate warming, has been advanced as a test case of this phenomenon. However, prior work largely ignores the broad, polyphagous diet of these caterpillars. The ability to use a range of host-plants has the potential to buffer caterpillars against mismatch, but there has hitherto been no major systematic assessment of caterpillar performance on different hosts and how adaptation to locally abundant host-plant species may act to modulate and optimise performance in different populations. Here, I tested the performance of winter moth caterpillars across nine host-plant species from four geographically disparate British caterpillar populations. I found that caterpillars perform well across a range of host-plants and that, contrary to the assumption made widely in the literature, oak is a relatively poor host-plant species. There is clear evidence of population specific variation in performance on different host-plants, consistent with genetic divergence. Occupying a broad trophic niche—as in the case of the winter moth—might help species exploit a narrow phenological niche, and withstand uncertainty and changes introduced by environmental and climatic variation.

2.2. Introduction

Over recent decades, global climatic change, in the form of rising temperatures (IPCC, 2021), has brought about consistent changes in the phenology of many species, across a range of taxonomic groups (Thackeray *et al.*, 2016; Cohen *et al.*, 2018; Roslin *et al.*, 2021). For many organisms, successfully timing a particular stage in their life history involves synchronising their phenology with a stage in the life history of another species. Certain fish, for example, that fail to spawn at the correct time can find their offspring mismatched with the maximum abundance of a food supply, with negative consequences for recruitment to the population (Cushing, 1990). Similarly, birds that mistime their breeding relative to the maximum availability of an ephemeral food supply can suffer reductions in offspring condition (Samplonius *et al.*, 2016), individual fitness (Reed *et al.*, 2013), and perhaps even population size (Both *et al.*, 2006; Mclean *et al.*, 2016; though cf. Samplonius *et al.*, 2020). There is a growing concern among ecologists that divergent phenological responses across different species to global temperature changes may lead to a temporal decoupling of many such timed interactions, with potentially catastrophic effects on individual populations and, indeed, whole ecosystems (reviewed in Samplonius *et al.*, 2020).

In a trophic context, phenological mismatch is most likely to occur where species exploit a single, ephemeral resource—this makes precise timing particularly important, and even small temporal misalignments can theoretically result in significant negative fitness effects (Hjort, 1914; Cushing, 1967, 1969, 1990; Durant *et al.*, 2007). Most prior research which attempts to evaluate the significance of trophic mismatch has focussed on simplified food-chains. In particular, the winter moth *Operophtera brumata*—an abundant Holarctic geometrid—has become a standard study organism for the effects of climate change on spring phenology, phenological synchrony, and the possible role of climate warming in inducing phenological mismatch among interacting taxa (Charmantier *et al*., 2008; Visser *et al.*, 2021). Due to its preponderance in the spring caterpillar fauna of temperate woodlands—where it can often be overwhelmingly abundant—the winter moth is often taken as representative of the primary consumer level in the well-studied tree/caterpillar/bird food-chain (Charmantier *et al.*, 2008; Cole *et al.*, 2015, 2021; Hinks *et al.*, 2015; Shutt, 2017; Shutt *et al.*, 2019a; Visser *et al.*, 2021). Hatching just as the foliage begins to appear on plants in early spring (Skinner, 2009), winter moth caterpillar occurrence coincides with the this newly available resource.

Over the last few decades, evidence has accumulated that seems to suggest that the fitness of winter moth caterpillars depends to a very large extent on precisely matching their phenology with that of their host-plants (Feeny, 1970; Wint, 1983; Kerslake and Hartley, 1997; Tikkanen *et al.*, 1998; Buse *et al.*, 1999; Tikkanen and Lyytikäinen-Saarenmaa, 2002; Tikkanen and Julkunen-Tiitto, 2003; Van Dongen, 2006; van Asch and Visser, 2007). Caterpillars which hatch too early find themselves with no foliage to feed on and starve (Wint, 1983); those hatching later (which might intuitively appear the safer strategy) are forced to feed on more mature foliage which has undergone structural changes and accumulated secondary chemicals reducing its nutritional value, and hence its palatability (Feeny, 1968, 1970). The result is strong stabilising selection for close synchrony between the timing of caterpillar egg hatch and the timing of bud-burst on their host-plants (Tikkanen and Julkunen-Tiitto, 2003; van Asch *et al.*, 2007). Indeed, van Asch *et al*. (2007) estimated that the fitness of caterpillars eclosing as little as five days early or five days late on oak would decline to almost zero. But this framing of the winter moth as reliant on synchrony with a single host-plant species (Table 2.1) misrepresents the diet of this species—rather, in nature, we find a complex food web of many different interacting species.

Temperate spring-feeding caterpillars as a group are typically polyphagous trophic generalists. Polyphagy in the winter moth has long been acknowledged anecdotally (Stainton, 1859; Meyrick, 1895, 1928; Stokoe, 1948a; Allan, 1979; Maitland Emmet and Heath, 1992; Porter, 2010; Waring *et al.*, 2017; Henwood *et al.*, 2020) and the caterpillars have been recorded feeding on plants from 31 different genera across 15 families, on species as diverse as birch *Betula*, heather *Calluna vulgaris*, and bilberry *Vaccinium myrtillus* (Robinson *et al.*, 2010). Occupying a broad niche can be optimal in uncertain environments (Levins, 1968) and so, faced with uncertainty in various aspects of the environment—such as the unpredictability of the developmental stage of any available leaves at the onset of spring—broad, polyphagous diets might have arisen in these species as a buffer against being mistimed with any one particular host-plant individual or species. Despite this, very few studies considering the ecological significance of phenological asynchrony explicitly investigate the extent to which consumers are generalists (Samplonius *et al.*, 2020).

Table 2.1. The role of oak in the life of the winter moth: a selection of the phenological literature. There is a general consensus among widely cited studies that English oak *Quercus robur* is the most important, and preferred, host-plant of the winter moth in the field. Number of citations shown underlined after reference, obtained from Google Scholar (accessed 3 February 2023).

Views on the role of oak *Quercus robur* as a host-plant

"For example, winter moth (*Operophtera brumata* L., Geometridae) larvae develop into heavier pupae when fed on young oak leaves than when reared on hazel (*Corylus avellana* L.) or blackthorn (*Prunus spinosa* L.), two species commonly used as host plants in the field (G. R. Gradwell, personal communication)"
Feeny (1970), 2404

"Larvae of the winter moth are able to feed on a wide range of trees and shrubs, but they are especially abundant on oaks (*Quercus robur*), which they sometimes defoliate."
Varley *et al.* (1974), 1101

"Most of these losses are related to the degree of asynchrony between larval eclosion and the bud burst of the primary food-plant (*Quercus robur*)."
Wint (1983), 143

"The winter moth *Operophtera brumata* is one of the most common forest insects in Central Europe. The larvae feed on the oak, *Quercus robur*, as well as on several other species of broad-leaved trees."
Kirsten and Topp (1991), 24

"The synchrony between the emergence of larval winter moth (*Operophtera brumata* L.) and budburst of pedunculate oak (*Quercus robur* L.), its primary host (Wint, 1983), is critical for the moth's success."
Buse and Good (1996), 171

"*Operophtera brumata* L. [is] one of the most important herbivores of oak."
Dongen *et al.* (1997), 139

"*Operophtera brumata* L. (Lepidoptera: Geometridae) is one of the most abundant insect herbivores on *Q. robur*."
Tikkanen and Julkunen-Tiitto (2003), 174

"*Operophtera brumata* is a polyphagous moth that is able to feed on a range of tree and shrub species (Holliday, 1985). In the U.K., oak *Quercus* spp. (Fagaceae) and other deciduous trees are regarded as the optimal hosts of this insect (Feeny, 1970; Wint, 1983; Holliday, 1985), but *O. brumata* has also been recorded on heather *Calluna vulgaris* (Ericaceae) where it reaches outbreak densities (Picozzi, 1981; Kerslake *et al.*, 1996)."
Vanbergen *et al.* (2003), 55

cont.

"Timing of egg hatching in *O. brumata* is itself under selection for synchronization with bud burst in oak trees (*Quercus robur*). Caterpillars of this moth rely on oak leaves for food, and although the oak trees have been opening their buds earlier, advancement in the date of egg hatching has been more extreme."
"Our fitness estimations are based on the assumption that the optimal moment of egg hatch is determined by the moment of *Q. robur* bud burst. *O. brumata* is not a specialist species: it can also feed on leaves from tree species other than oak."
van Asch *et al.* (2007), 252

"Pedunculate oak, *Quercus robur*, is a favoured host of winter moth"
Singer and Parmesan (2010), 324

"However, caterpillars [of the winter moth] are available to the birds only during a brief period in spring, as the larvae exploit the newly emerged leaves of their host trees (predominantly oak *Quercus* spp.; Varley and Gradwell 1958)"
Hinks *et al.* (2015), 68

"Pedunculate oak is described as the primary host plant of winter moth throughout its native range."
O'Donnell *et al.* (2019), n/a

Table 2.1 cont.

In the case of the caterpillars of the winter moth, their highly polyphagous diet has seldom been considered in the phenological literature, or given only a passing reference (Table 2.1). Instead, the focus has mainly been on a single host-plant, oak—specifically the English oak *Quercus robur* (Table 2.2; Roland and Myers, 1987; Buse et al., 1998, 1999; Tikkanen and Lyytikäinen-Saarenmaa, 2002; Tikkanen and Julkunen-Tiitto, 2003; Van Dongen, 2006; van Asch et al., 2007; Mannai et al., 2017; Kulfan et al., 2018). The reasons for this emphasis seem to be largely historical, and can be traced back to the earliest considerations of phenological synchrony in the winter moth (e.g. Thomson, 1954; Feeny, 1968; Varley et al., 1974; Dongen et al., 1997). The focus on oak gives the impression of this species facing an ephemeral and moving resource peak in spring (young oak foliage), as the oak itself responds plastically to temperature (Burgess *et al.*, 2018). On the other hand, if winter moths can feed on a wide range of plant species that vary in their leafing phenology then this raises the prospect that trophic generalism might actually serve as a buffer on that mismatch.

Despite the extensive literature on the winter moth, the relative impacts of different host-plant species on larval performance in the field remains unclear. Experimental studies tend to consider performance on a single host-plant species (predominantly *Q. robur*), a range of

Table 2.2. Taxonomic coverage of the literature on winter moth caterpillar performance across host-plants. Studies are grouped by those which consider the effects of varying degrees of asynchrony on performance across host-plant species and those which consider performance at one time point only. Particularly in studies of synchrony, there is a clear bias towards oak *Quercus*. The inclusion of a host-plant species in a particular study is indicated by ✓. Taxa arranged alphabetically below within higher groupings. Performance Metrics used are: S (survival); P (pupal mass); GR (growth rate); DI (development index); DT (development time); FAb (abundance across host-plants measured in the field); LP (larval choice experiment); FU (food utilisation or assimilation rate); FP (frass production); F (fecundity); and MO (mass of ova).

				ADOXACEAE	**ERICACEAE**				**BETULACEAE**											**FAGACEAE**									**GROSSULARIACEAE**	**SALICACEAE**												**MALVACEAE**		**OLEACEAE**	**PINACEAE**	**RHAMNACEAE**	**ROSACEAE**										**ULMACEAE**	**SAPINDACEAE**		
				Sambucus	Calluna	Vaccinium			Alnus		Betula						Carpinus	Corylus	Ostrya	Fagus	Quercus								Ribes	Populus	Salix											Tilia		Fraxinus	Picea	Rhamnus	Crataegus	Malus				Prunus			Rubus	Sorbus	Ulmus	Acer		
First Author	**Year**	**Country**	**Performance Metric**	racemosa	vulgaris	angustifolium	corymbosum	myrtillus	incana	glutinosa	spp	nana	papyrifera	pendula	pubescens	ssp. czerepanovii	betulus	avellana	virginiana	sylvatica	afares	canariensis	cerris	garryana	pubescens	robur	rubra	suber	spp.	tremula	alba alba	alba vitellina	aucuparia	caprea	fragilis	myrsinifolia	pentandra	phylicifolia	triandra	viminalis	x rubens	americana	cordata	excelsior	sitchensis	frangula	monogyna	domestica	sylvestris	sp. (crab apple)	spp.	padus	pensylvanica	spinosa	idaeus	aucuparia	americana	platanoides	pseudoplatanus	rubrum
Performance effects of asycnhrony examined																																																												
Feeny	1970	UK	P																							✓																																		
Wint	1983	UK	S, P, DT, LP															✓		✓						✓																						✓		✓					✓						
Watt	1991	UK	S																																										✓															
Hunter	1991	UK	P																																										✓															
Kirsten	1991	Germany	P, GR, F																							✓					✓	✓		✓	✓				✓	✓	✓																			
Kerslake	1997	UK	S, P, GR, DI		✓																																																						
Van Dongen	1997	Belgium	P																							✓																																		
Buse	1999	UK	P																							✓																																		
Tikkanen	2002	Finland; Denmark	P, GR, DT																							✓																									✓								
Tikkanen	2003	UK	S, F																							✓																																		
Van Dongen	2006	Belgium	P																							✓																																		
van Asch	2007	Netherlands	S, P																							✓																																		
Wesołowski	2008	Poland	FAb																							✓																																		
Kulfan	2018	Slovakia	FAb																				✓		✓																																		

cont.

Table 2.2. *cont.*

				ADOXACEAE	**ERICACEAE**				**BETULACEAE**												**FAGACEAE**									**GROSSULARIACEAE**	**SALICACEAE**												**MALVACEAE**		**OLEACEAE**	**PINACEAE**	**RHAMNACEAE**	**ROSACEAE**										**ULMACEAE**	**SAPINDACEAE**		
				Sambucus	Calluna	Vaccinium			Alnus		Betula						Carpinus	Corylus	Ostrya	Fagus	Quercus									Ribes	Populus	Salix											Tilia		Fraxinus	Picea	Rhamnus	Crataegus	Malus				Prunus			Rubus	Sorbus	Ulmus	Acer		
First Author	**Year**	**Country**	**Performance Metric**	racemosa	vulgaris	angustifolium	corymbosum	myrtillus	incana	glutinosa	spp	nana	papyrifera	pendula	pubescens	ssp. czerepanovii	betulus	avellana	virginiana	sylvatica	afares	canariensis	cerris	garryana	pubescens	robur	rubra	suber	spp.	tremula	alba alba	alba vitellina	aucuparia	caprea	fragilis	myrsinifolia	pentandra	phylicifolia	triandra	viminalis	x rubens	americana	cordata	excelsior	sitchensis	frangula	monogyna	domestica	sylvestris	sp. (crab apple)	spp.	padus	pensylvanica	spinosa	idaeus	aucuparia	americana	platanoides	pseudoplatanus	rubrum
Performance at only one time point considered																																																												
Cuming	1961	Canada	FAb																✓								✓															✓									✓						✓			✓
Warrington	1985	UK	P, GR																																																								✓	
Roland	1987	Canada	P																					✓																								✓												
Kerslake	1996	UK	S, P GR, DI		✓			✓																																																				
Kerslake	1998	UK	S, P GR, DI		✓																																																							
Buse	1998	UK	P, DT, FU, FP, F, MO																							✓																																		
Lavola	1998	Russia	LP											✓																																						✓								
Tikkanen	1998	Russia	FAb	✓					✓						✓											✓			✓	✓			✓	✓												✓						✓						✓		
Tikkanen	1999	Russia	S, FAb	✓					✓					✓	✓			✓								✓			✓	✓			✓	✓		✓		✓								✓						✓			✓	✓		✓		
Tikkanen	2000	Finland	S, P, GR, DT																							✓				✓								✓														✓								
Ruuhola	2001	Finland	GR																																	✓	✓	✓																						
Vanbergen	2003	UK	S		✓																					✓																			✓															
Strengbom	2005	Sweden	S, P					✓																																																				
Wesołowski	2006	Poland	FAb							✓	✓						✓	✓								✓				✓													✓	✓														✓		
Belsing	2015	Norway	S, P					✓				✓				✓																																												
Pepi	2016	Canada	S																								✓																					✓												✓
Mannai	2017	Tunisia	S, DT, FAb																		✓	✓						✓																																
O'Donnell	2019	USA	S, P, GR, FAb			✓	✓						✓														✓																					✓		✓			✓							✓

species at a single geographical site, or a small selection of species across relatively proximate geographical populations (see Table 2.2). Performance on some very widespread, abundant plant species—which are likely significant hosts in the wild, e.g. *Betula* spp.—has been investigated only a handful of times. Despite the Holarctic distribution of the winter moth, and the considerable variation in the flora occurring throughout that distribution, previous studies considering local adaptation to host-plant species between sites are typically limited in geographical scale (e.g. Kerslake and Hartley, 1997; Tikkanen et al., 2000). There is therefore very limited evidence as to both the geographical scale of any local adaptation and the magnitude of any differences in fitness effects. Since female winter moths appear during the winter months and, being flightless, likely exercise very little discrimination with regard to the host-plant that their offspring will find themselves on, if populations were locally adapted, we might expect performance on a given host-plant species to be roughly proportional to the relative abundance of that host-plant species in the local environment (see Appendix 10 for more discussion). A broad diet could give this species flexibility, with local adaptation potentially fine-tuning and optimising performance at a local level.

The fragmented and incomplete nature of our knowledge about such an emblematic species makes a systematic investigation and re-evaluation of the role of polyphagy in its life history a pressing concern. Here, I aimed to quantify the performance of winter moth caterpillars across a range of common, widespread host-plant species, testing one of the foundations of the hypothesis that polyphagy might serve as a buffer against phenological mismatch with host bud-burst. To do so, I conducted an extensive assay of performance across several metrics (survival, pupal mass, development time, and estimated fitness) on nine host-plant species, using 3600 individual caterpillars. I obtained livestock from four winter moth populations across the UK and tested whether performance on host-plants was analogous across populations or whether there were population-specific differences consistent with genetic divergence. I consider these results within the context of the patchy existing literature (Table 2.2) and what their implications might be for the resilience of winter moth populations (and the food webs of which they form a crucial part) in the face of the varying phenological responses to climate change observed across these different taxa.

2.3. Methods

2.3.1. Source populations

I obtained winter moth ova from four populations across Great Britain (Table 2.3). Using lobster-pot style trunk traps, modelled on those described by Varley *et al.* (1974), which intercepted females as they ascended trees after eclosion (Appendix 9), I collected 165 female winter moths from 25 Nov 2019 to 8 Jan 2020, across 72 traps. Entomologists from three other UK sites each provided me with a minimum of fifteen female winter moths. These individuals were collected using manual methods of searching forested areas in the hours after dusk by torchlight.

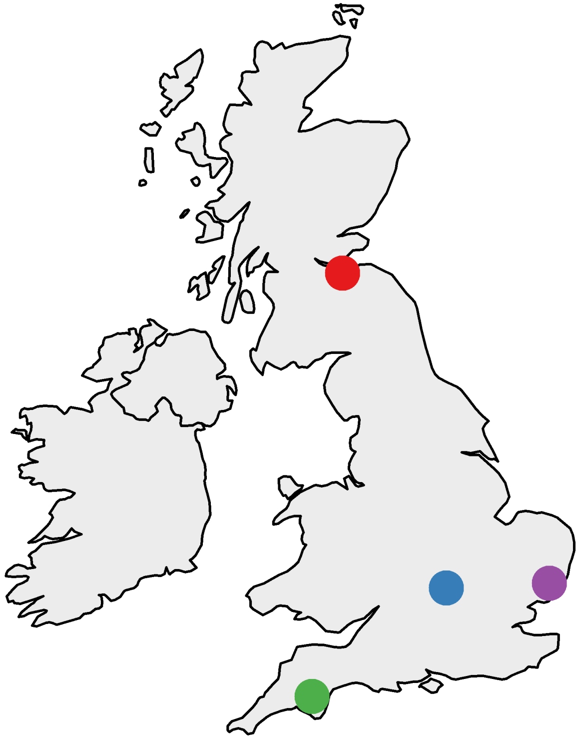
2.3.2. Rearing methodology

After collection females were placed individually in 75 x 25mm glass phials with a wad of cotton at the bottom to act as an egg-laying medium. Previous trials suggested that cotton resulted in individuals laying the maximum number of eggs relative to a range of other commonly used media. Females were stored at ~5°C in complete darkness and allowed to lay freely. Approximately one month later, all tubes were examined and the dead females were removed. Ova from a total of 126 females from the Edinburgh site, 15 from Buckinghamshire, 14 from Devon, and 19 from Suffolk were obtained.

When foliage became available in spring, ova were removed from cold storage and placed at room temperature (~20°C) to stimulate egg hatching. A subset of ova, sampled from across all broods, were removed concurrently and allowed to hatch. The fact of their being exposed to relatively high temperatures helped ensure individuals hatched at the same time, despite inter- and intra-brood variation in the temperature requirements for eclosion. Larvae were assigned at random from each brood to each treatment group, and subsequently to each rearing culture within that treatment group.

Larvae were reared in mixed-brood groups of twenty individuals (a “culture”), firstly in small 75 x 50 x 15mm transparent plastic containers and then, at around the third instar, in larger 500ml disposable plastic food containers (Figure 2.1). Cultures were established concurrently from caterpillars hatched in the previous 24hrs. The rearing containers were lined with white absorbent paper towels. Freshly excised food was placed in each container and examined

Table 2.3. Summary of UK collection sites of winter moth livestock used in the host-plant assay, with a description of the local flora. Geographical location of each is shown on the map.



	Site	Co-ordinates	Habitat Characteristics
●	BUCKINGHAMSHIRE Hill Farm Cottage, Buckingham (VC 24)	51.978946°N -0.983623°E	Hamlet surrounded by grazing pasture. Small garden orchard of apple, pear, plum, cherry, fig and apricot. Dry area, with extensive hedges of hawthorn, maple, ash, blackthorn. 110m
●	DEVON Dart Valley Nature Reserve, Poundsgate (VC 3)	50.530946°N -3.849855°E	Ancient, damp, primarily oak woodland, situated in heathland. 280m
●	EDINBURGH Hermitage of Braid LNR, Edinburgh (VC 83)	55.919501°N -3.197014°E	Exposed patch of mature oaks on the edge of a large mixed woodland, adjacent to grassland. Sycamore abundant throughout. 105m
●	SUFFOLK Ipswich Golf Course, Ipswich (VC 25)	52.042964°N 1.215717°E	Sheltered site at the edge of a mixed woodland of oak, birch, sycamore, Scots pine. Surrounded by dry heathland and short-cropped grassland. 20m

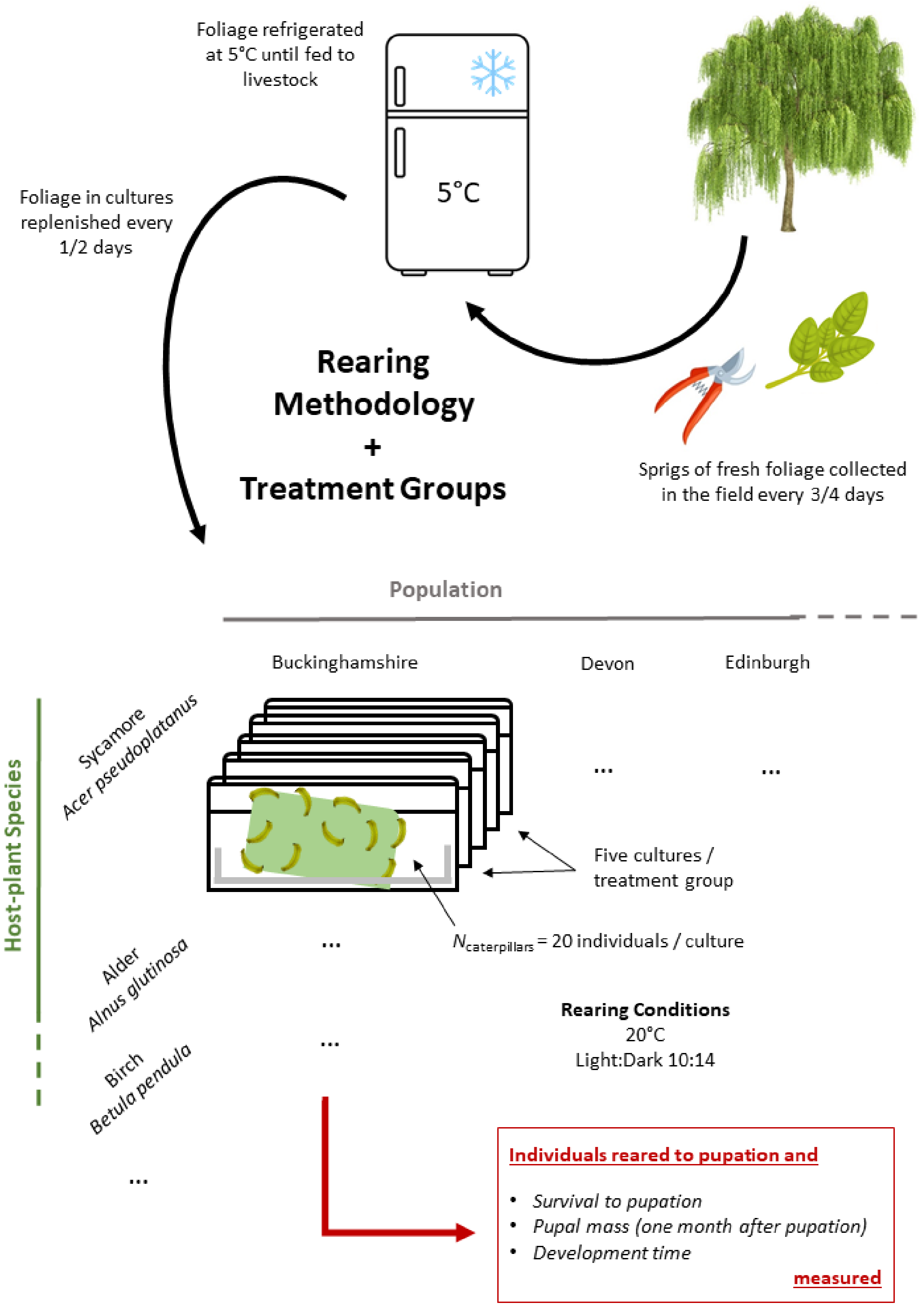


Figure 2.1. Schematic of experimental design for Chapter 2. Livestock of the winter moth *Operophtera brumata* collected from four British populations were reared to pupation on foliage from across nine different host-plant species. Caterpillars were reared in cultures of 20 individuals. Performance in each host by population treatment was quantified on three metrics.

daily to check its condition and how much remained. Typically it was replaced daily, no less than every second day (Figure 2.1). Caterpillars were provided with an excess of plant material at all times such that the quantity of food was never a limiting factor to growth. The tissue lining of the container was replaced each time new food was provided. Caterpillar rearing cultures were maintained at room temperature (~20°C), with a 10:14 light/dark regime.

At the completion of their development the caterpillars pupated in the tissue at the base of the container. After all larvae had pupated, excess host-plant material was removed and the containers were stored at room temperature. One month after pupation, pupae were removed, laid out on cotton for emergence in sealed plastic container, and stored outdoors under a canopy at ambient environmental temperature.

2.3.3. Host-plant assays

The aims of this experiment were twofold: firstly, to determine how caterpillar performance differed among nine common host-plant species; and secondly, if performance differed across the different geographical populations in a manner consistent with local adaptation. Nine known host-plant species of the winter moth (Robinson *et al.*, 2010) which are common and widespread in Britain were selected for use in the assays: alder *Alnus glutinosa*, apple *Malus domestica*, birch *Betula pendula*, cherry *Prunus avium*, hawthorn *Crataegus monogyna*, oak *Quercus robur*, sallow *Salix caprea*, sycamore *Acer pseudoplatanus*, and willow *Salix alba* (Appendix 7). One hundred larvae from each source population were randomly assigned from across broods to each of the nine host-plant species, at twenty larvae per rearing culture (Figure 2.1). In total, 3600 caterpillars were used in this experiment. Since it seems likely that caterpillar fitness on foliage changes as it matures, the calendar start date of each host-plant treatment was staggered, such that in the case of each host-plant species the experiment began when a sufficient number of individual trees could be sampled in the field at an appropriate phenological stage (Bud Stage 4, Table 4.2; see Appendix 1, Table S2.1). Fresh foliage was collected from a dozen individual trees of each species every four to five days as cut sprigs 15cm long and stored in airtight plastic bags at ~5°C in a Russell Hobbs RHCLRF17 tabletop refrigerator until required for feeding, to maintain freshness. Foliage was collected from trees near Falkirk (Stirlingshire; 56.069°N, -3.767°E) and Kincardine (Fife; 56.057°N, -3.613°E).

The secondary chemistry of plant leaves can vary not only between species, but also individuals due to factors such as differing environmental conditions, soil chemistry, local geology, and associated plant species (e.g. Laitinen *et al*., 2005; Lindroth, 2012; Kos *et al*., 2015). This variation can affect the fitness of insects feeding on those leaves. In order to minimise the effects of individual variation in leaf properties *within a host species*, leaves from across all the sampled tree individuals were randomly assigned to each rearing culture, such that larvae at any one time had access to foliage from a range of different host-plant individuals belonging to the same species. This reduced the likelihood of a single poor host-plant individual markedly affecting any particular rearing culture.

The performance of caterpillars in each treatment group was quantified by measuring: the survival of each individual from hatch to pupation; the final pupal mass attained by each individual one month after pupation (measured using a Mettler AJ50 balance); and, the time taken for caterpillar development from egg hatch to pupation. Since larvae were reared in groups it was not possible to relate each of these values to a specific individual.

2.3.4. Statistical analyses

Analyses of larval performance were conducted in *R* v.4.0.3 using MCMCglmm (Hadfield, 2010). Survival to pupation ("Surv"), pupal mass ("Mass"), and development time ("Dev Time") were each modelled separately in binomial and Gaussian generalised linear mixed models, respectively. I constructed the model so as to test for: overall differences in performance between host-plants across all populations; intrinsic differences in performance of caterpillars derived from particular populations; and, geographical divergence in performance between populations consistent with local adaptation (Table 2.4; see also Blanquart et al., 2013). In the Mass model, sex was included as an additional random effect because this could be determined by sexing the pupae and mass almost certainly varies by sex. Variance components were estimated on the link scale for each model. All models were run for 1500000 iterations with a 500000 burn-in and thinning every 100 iterations. In the binomial model for survival, default priors were used for the fixed effects (mean = 0, with a large variance), inverse Wishart priors for the random effects, and the residual variance was fixed. In the remaining Gaussian models, the default priors were used throughout. Using the posterior distributions of survival, pupal mass, and development time I also estimated the

Table 2.4. Modelling the effects of host-plant on winter moth caterpillar performance, measured as survival to pupation, development time, and pupal mass. Justification gives the hypothesis tested by each term. A significant Host-plant:Population interaction would be consistent with local adaptation (though not proof of it)—a significant effect of population, on the other hand, would perhaps indicate flaws in the experimental procedure, particularly if the performance was highest in the population most proximate to the rearing site (Edinburgh). ^ indicates as above.

Response Variable	**Random Effect Term**	**Justification**
Surv/Dev. Time	Host-plant	Tests whether performance is consistently higher on certain host-plant species across all four populations
	Population	Tests whether performance is consistently higher in caterpillars from certain populations across all host-plant species. This shows whether, for example, individuals from some populations are performing consistently better in the common garden environment (e.g. perhaps populations closer to that site would perform better than those collected from farther away, due to, e.g., adaptation to weather conditions, clines in host-plant traits, etc.)
	Host-plant:Population	Tests whether performance on certain host-plants is population specific, i.e. do caterpillars from one population perform better on a particular host-plant species that those from another population
	Rearing Culture	Tests whether performance is consistently higher in individuals reared in the same captive environment, a “culture”
Mass	Host-plant	^
	Population	^
	Host-plant:Population	^
	Sex	Tests whether performance is consistently higher in one sex compared with the other
	Rearing Culture	^

rate of development (mg/day) and absolute fitness in each treatment group (see Appendix 2 for an explanation and the detailed methodology used to calculate fitness).

2.4. Results

2.4.1. Caterpillar performance and fitness across host-plant species

2.4.1.1. Survival

Overall mean individual probability of survival to pupation across all treatment groups was 0.18. Survival probability varied significantly across host-plant species (Figure 2.2; 47.20% of variance on the link scale, CIs: 19.07, 78.59). This was likely accounted for by several species which depart from the mean by an unusual degree. Relative to oak (0.16, CIs: 0.06, 0.27), survival is lower on alder (0.03, CIs: 0.00, 0.06) and hawthorn (0.04, CIs: 0.00, 0.07) and markedly higher on willow (0.47, CIs: 0.30, 0.65), but does not vary significantly between oak and the remaining host species (Figure 2.3).

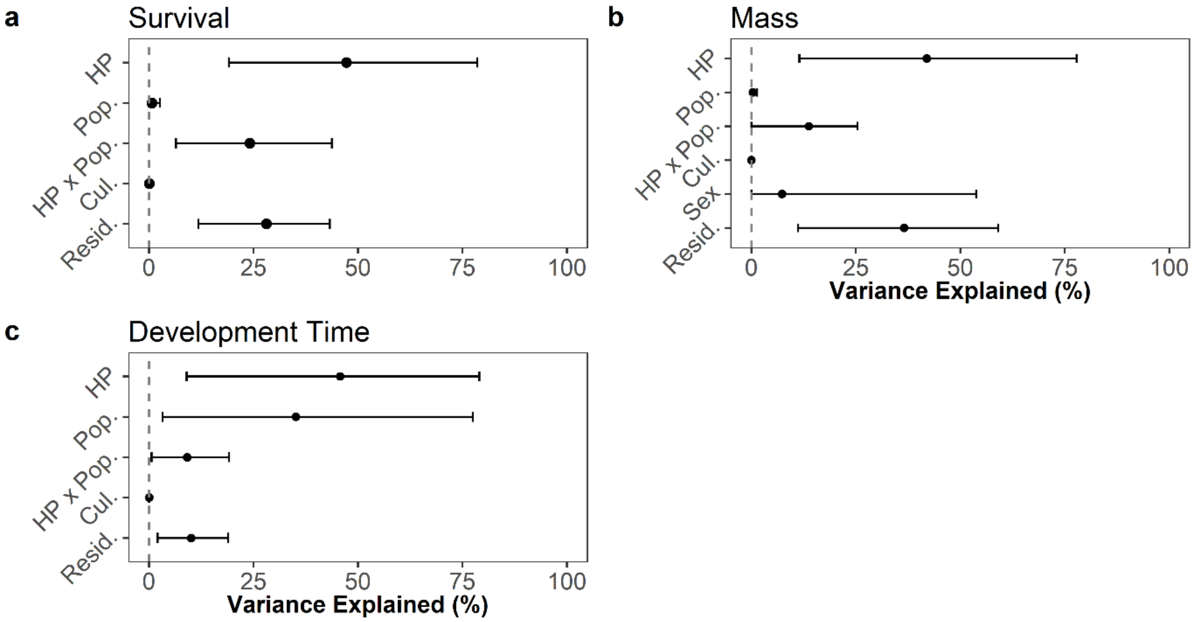


Figure 2.2. Variance components of caterpillar performance across host-plants and populations. Relative percentage (+/- 95% CIs) contribution of different effects to overall variance explained by (a) survival, (b) development time, and (c) mass models (Model 4). Culu (rearing culture); Resid. (residual variation); HP (host-plant species); Pop. (population); HP x Pop. (host by population interaction effect); Sex (individual sex). Estimates shown on the link scale.

2.4.1.2. Pupal mass

Mean pupal mass across all treatment groups one month after pupation was 26.17mg (sd = 7.55). Female pupae (26.80mg, sd = 8.10) were heavier on average than those of males (25.6mg, sd = 7.01). Pupal mass varies significantly among host-plant species (Figure 2.2; 42.33% of variance, CIs: 12.19, 78.19). Pupal mass is significantly higher on all host-plant species, relative to oak (Figure 2.3). Host-plant species fall into three discrete groups with regard to pupal mass attained, with apple and cherry being intermediate between oak and all the remaining species (Figure 2.3).

2.4.1.3. Development time

Mean development time across all treatment groups was 32.14 days (sd = 6.54). Development time varies significantly by host-plant species (Figure 2.2; 45.73% of variance, CIs: 8.94, 79.00). There is a range of variation between different host-plant species—although development time on oak does not differ significantly from the mean, it is significantly shorter than on some other host-plants, such as hawthorn, apple, and cherry (Figure 2.3).

2.4.1.4. Estimated rate of development

Mean rate of development across all treatment groups was 0.76 mg/day (CIs: 0.50, 1.09). On a majority of host-plant species, estimate rate of development does not differ significantly from the mean (Figure 2.3). It is however significantly higher on willow 1.03 mg/day (CIs: 0.78, 1.34) and lower on apple (0.56, CIs: 0.43, 0.72) and cherry (0.52, CIs: 0.41, 0.66). Notably, there is no significant difference between the development rate on oak (0.74, CIs: 0.44, 1.11) and all other host-plant species (Figure 2.3)—this suggests that caterpillars are not growing more rapidly on oak even though they show a tendency to shorter development times on that host.

2.4.1.5. Fitness

Arithmetic mean estimated fitness (eggs per female, see Appendix 2) across all treatment groups was 22.19 (sd = 31.80). Fitness was significantly higher than average on birch (44.87, CIs: 16.65, 81.85) and willow (94.29, CIs: 45.62, 144.89), and lower on oak (4.66, CIs: 0.46, 11.59), alder (2.20, CIs: 0.29, 5.99), and hawthorn (2.66, CIs: 0.38, 6.82). Relative to oak, fitness is higher on birch and willow—two abundant and widespread species (Figure 2.3).

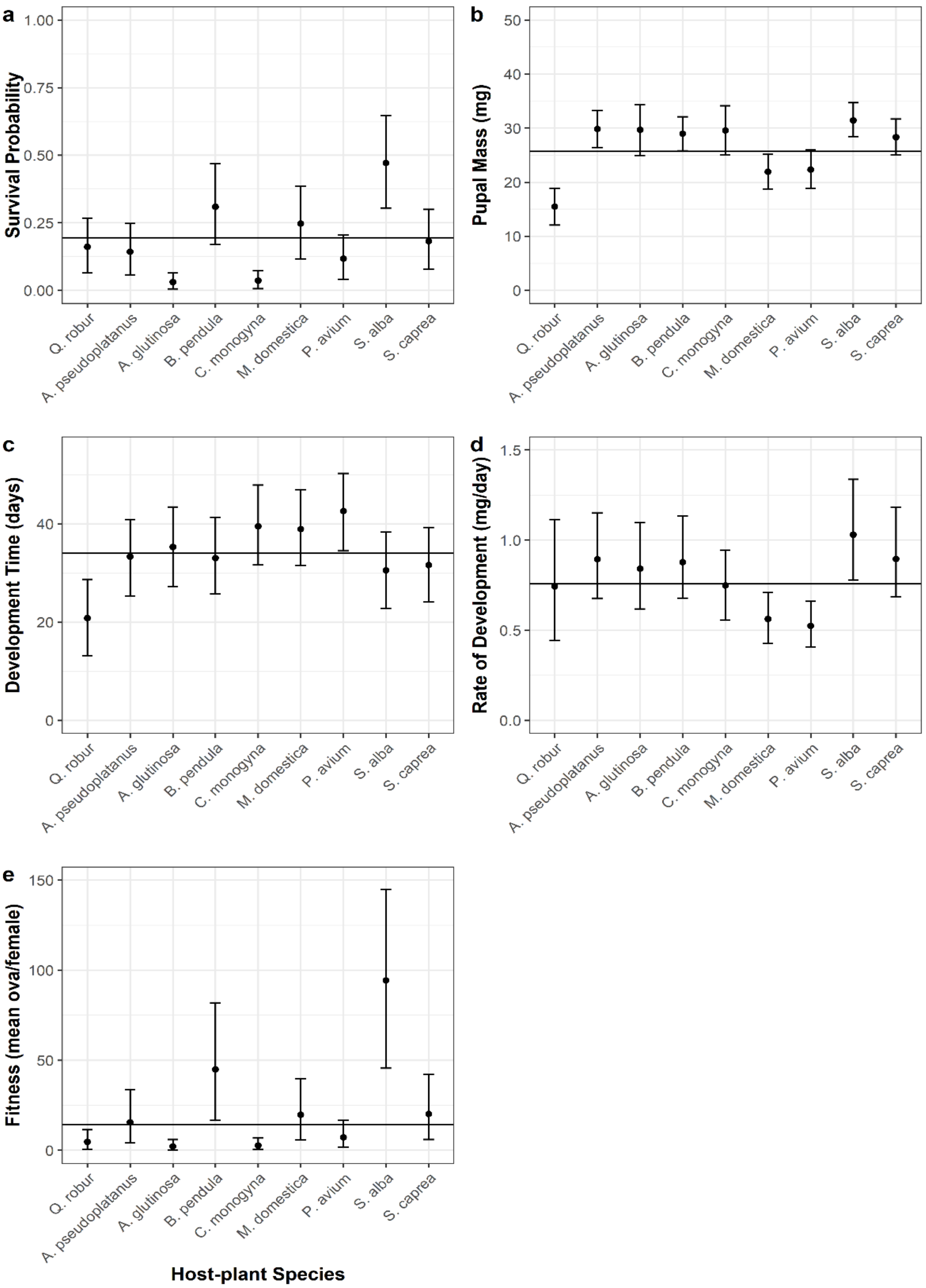


Figure 2.3. Overall winter moth performance on different host-plants, across all sampled populations. Performance quantified as (a) survival probability, (b) pupal mass, (c) development time, (d) rate of development, and (e) estimated fitness. Mean estimates and 95% credible intervals shown. Global mean for each performance metric shown by solid line.

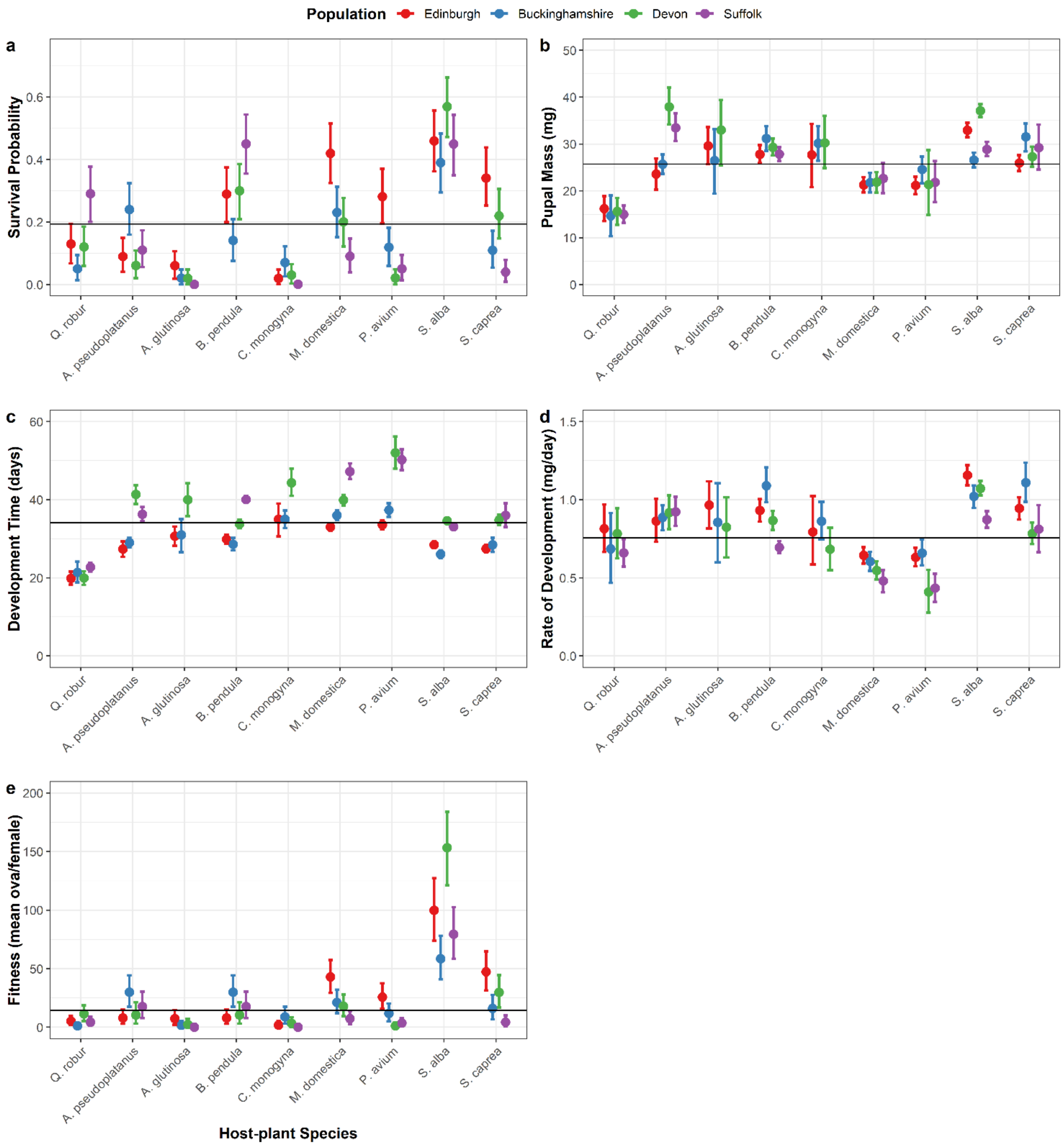


Figure 2.4. Winter moth performance in each host-plant by population treatment group. Performance quantified as (a) survival probability, (b) pupal mass, (c) development time, (d) rate of development, and (e) estimated fitness. Mean estimates and 95% credible intervals shown. Global mean for each performance metric shown by solid line.

2.4.2. Geographical divergence in caterpillar performance

Source population alone explains a significant quantity of variation only in development time (Figure 2.2; 35.14%, CIs: 3.17, 77.49), which is generally more prolonged in livestock sourced from the Devon and Suffolk populations (Figure 2.4; Appendix 1, Figure S2.1). This suggests that, in the common garden setting of this experiment, there are largely no systematic effects of source population. Although development time is generally more protracted in these two populations, between-population differences in development rate are less obvious and less pronounced (Figure 2.4).

The host by population interaction effect explains a significant or substantial quantity of variation in survival (24.08, CIs: 6.41, 43.71), pupal mass (13.62, CIs: 0.00, 25.48), and development time (9.08, CIs: 0.57, 19.15) (Figure 2.2). This effect indicates differences in performance on the same host-plant species among source populations—suggesting genetic divergence in performance, and perhaps local adaptation. Although performance on a given host-plant does apparently vary considerably among populations, there is no clear evidence of local adaptation along these lines across all performance metrics (including estimated fitness) based on the floral composition of each site (Table 2.3). The relative prevalence of the different plant species at each site does not obviously match those species on which fitness is highest (cf. Figure 2.4 with Table 2.3)

2.5. Discussion

2.5.1. The significance of oak as a host-plant of the winter moth

In this experimental study of performance using 3600 caterpillars from four British populations on nine host-plant species, I found that oak is largely unexceptional as a host-plant. This runs counter to the common framing of English oak (*Q. robur*) as the most significant host-plant species for the caterpillars of this moth in the wild (Table 2.1). In two respects oak does stand out, but as a relatively poor host-plant. First, I found that developmental time—a well-established, though inconsistent, signifier of environmental stress in Lepidoptera (Goulson and Cory, 1995; Awmack and Leather, 2002; York and Oberhauser, 2002)—is considerably shorter on oak than on all other host-plant species, and no compensatory effect of rate of development was observed (Figure 2.3). Second, pupal mass is significantly lower on oak, producing females with a greatly reduced fecundity (Figure 2.3). Mean estimated fitness lags far behind many species, at the third lowest level attained in this experiment. Indeed, fitness is markedly higher on some of the other common, widespread host-plant species, such as birch (four times higher) and willow (eight times higher).

Previous experimental work, limited in geographical or taxonomic scope (Table 2.2), has found mixed results with respect to winter moth caterpillar performance across host-plants. In some cases performance is indeed highest on oak (Vanbergen *et al.*, 2003; O'Donnell *et al.*, 2019), and even on evolutionarily novel oak *Quercus* species (e.g. N. American *Q. rubra*; Embree, 1965, 1970) compared with natal host species such as apple *Malus.* In other instances alternative host-plant species prove equally suitable or more so—however, in a plurality of multi-species studies, oak results in average or mixed caterpillar performance, across a range of metrics (Cuming, 1961; Wint, 1983; Kirsten and Topp, 1991; Tikkanen *et al.*, 2000; Tikkanen and Lyytikäinen-Saarenmaa, 2002). Emphasising the complexity of the dietary ecology of this species, performance can vary significantly even in comparisons between oak species (Wesołowski and Rowiński, 2008; Kulfan *et al.*, 2018). Mannai *et al*. (2017) found that survival in each instar on different *Quercus* species can vary by tens of percent, as big a difference as was observed between different host-plant families and genera in my experiment. In the classic study by Wint (1983), often cited as evidence for the important role of oak as a host-plant, the picture too is mixed—while pupal mass was highest on oak, survival was higher on all other host-plant species assayed, barring beech *Fagus* and some hawthorn *Crataegus* treatments.

In light of this complex dietary ecology, illustrated by the results presented here, we ought to approach the existing literature on the consequences of phenological synchrony in this species, with its strong focus on oak (see Table 2.2), with some caution. Lab studies only capture one aspect of the ecology of a species: the palatability of the host-plant. In nature, different tree species and individuals, at different stages of growth, provide structurally different habitats, which might affect predation risk from vertebrates, parasitism, susceptibility to adverse abiotic conditions, etc. It would certainly be possible for extrinsic, non-dietary factors to differ sufficiently between host-plant species in the field that performance in the lab ran counter to abundance or prevalence observed in the field.

However, field studies comparing the abundance of winter moth caterpillars or defoliation across different host-plant species also find mixed results, with abundance being highest to mid-level on oak (Table 2.2, also see: Shutt, 2017; Shutt *et al*., 2019; Macphie *et al*., 2020). O'Donnell *et al.* (2019) found that while abundance in the field and performance in captive rearing experiments was higher on oak than on other host-plants, this was not to the same degree—the extent to which abundance was greater on oak in the field *exceeded* the differences in performance. We are presented, then, with a complex array of interacting factors: for example, the reduced development time that we see in oak might also reduce exposure to predation, potentially compensating for any loss in mass and fecundity. Such interactions might explain the apparent discrepancy between field and lab studies. Clearly, our knowledge of the dietary ecology of the winter moth, and other related species, is still incomplete and it is important that we expand our understanding of the relative significance in the field of alternative host-plant species. In particular, assessing any differences in the fitness effects of phenological asynchrony across these host species is an obvious direction for future work (see Chapter 3).

2.5.2. Evidence of local adaptation to floral composition

A winter moth caterpillar, newly hatching in spring, faces two principal uncertainties: the species of tree on which it will find itself, and the state of the developing foliage on that tree (if, indeed, the buds have broken sufficiently to make them accessible). Variation in both of these factors can result in significant variation in overall performance (see Chapters 3 and 4). Given that the ability of females to disperse is limited and that they seem unable to exert much, if any, host choice for their offspring (though see Connell, 2013), we might expect populations to adapt to locally abundant host-plant species which they are likely to frequently encounter. Although I find quite clear evidence of genetic divergence between the British winter moth populations studied in this experiment—in the form of strong host by population interaction effects on performance (Figures 2.2 and 2.4)—these differences in performance do not obviously conform with the predictions we might make based on the character of the flora at each collection site (Table 2.3). At a very local scale (under ~1km) we might reasonably predict relatively higher performance of winter moth caterpillars from Edinburgh and Devon on oak, for example, and from Buckinghamshire on various fruits, such as apple and cherry (Table 2.3). These patterns are not reflected in performance or fitness, however (Figure 2.4).

Systematic differences in survival on foliage between particular plant species in these assays can only be a consequence of differences in the mechanical properties of each leaf and the secondary chemistry—we can conveniently encapsulate the effects of both as *palatability* (Appendix 6). Relative phenological synchronisation, however, may be a more significant determinant of overall fitness on any given host-plant individual than palatability. Tikkanen and Julkunen-Tiitto (2003) for example found that asynchrony with bud-burst of 30 degree days could lead to a reduction in fitness of 50%. In the results I present here, with birch and willow being obvious exceptions, most host-plants show *no* significant deviation from the overall average of fitness, across host-plants (Figure 2.3). This would seem to support the notion that synchrony with host and therefore, by extension, synchrony with the mean phenology of a site (or that of a locally predominant host-plant species), is subject to greater selective pressure than physiological or morphological adaptations to maximise performance against the anti-herbivory defences of any particular plant species. It has even been suggested that synchronisation to host-plant is so important for fitness that the moths can adapt to a particular host-plant individual (Dongen *et al.*, 1997), and that this need has driven the evolution of flightlessness in the females, to inhibit gene flow and encourage extremely local adaptation (Feeny, 1970; see also Appendix 10). One reason that this seems unlikely though is that the taxonomically diverse nature of most woodlands—not only in the canopy but also among the understory and ground-level vegetation on which the caterpillars can feed—probably softens this kind of extreme divergent selection, as will gene flow introduced through male dispersal (van Dongen *et al.*, 1996; Legget *et al.*, 2011).

Adaptation solely to host-plant phenology, however, does not account for the substantial evidence that I find for geographical divergence in performance across host-plants (Figures 2.2 and 2.4). There are also several such instances in the literature: for example, in Karelia, larvae cannot establish on birch *Betula pendula* (Lavola *et al.*, 1998), but Belsing (2015) found survival rates on mountain birch *Betula pubescens* ssp. *czerepanovii* of around 40 per cent in northern Scandinavia, some thousand kilometres away. In the Karelian Isthmus, populations show relatively higher performance on bird cherry *Prunus padus*, an abundant regional host (Tikkanen *et al.*, 2000; Tikkanen and Lyytikäinen-Saarenmaa, 2002). Kerslake and Hartley

(1997) found that caterpillars derived from heather populations performed four times better, in terms of survival to pupation, on heather than on oak leaves (~10% vs ~40%). Naturally, these differences may be the result of a number of factors, such as different rearing techniques or abiotic conditions between studies, as well as the intrinsic palatability of the host-plant material. However, taken together, they suggest that some genetic divergence (perhaps attributable to local adaptation), does exist in this species, but that it is either in response to geographic variation in host-plant availability on a larger spatial scale than I considered here (Table 2.3), or some other geographically distributed variable (Appendix 10). An obvious line of future enquiry would be to characterise the flora of different populations at various spatial scales and examine the scale at which the local abundance of certain plant species best explained performance on those host-plants. This would necessitate a much greater level of population replication than I have been able to conduct here.

2.5.3. Polyphagy as buffering in an uncertain environment

It is apparent that, at some to some extent, trophic phenological synchrony is important for the winter moth. Any phytophagous insect species feeding in temperate climates necessarily is reliant to some degree on matching a temporally ephemeral *phenological niche*—foliage is not universally available throughout the whole year. That niche may be broad if any plant material can be consumed, or narrow if the insect is specialised on a particular plant, or a particular stage in the development of that plant. Hatching in early spring, as winter moth caterpillars do, and attempting to exploit young, newly available foliage, already narrows that niche substantially. As we see from studies on oak, selective pressures on timing resulting from variation in palatability can dictate an even narrower niche, allegedly on the order of several days (Tikkanen and Julkunen-Tiitto, 2003; van Asch *et al.*, 2007). Couple the apparent phenological specificity required to perform successfully on one particular host-plant species with the general complexity of the winter moth's environment—microclimatic variation in the temperature cues driving phenology; a patchy distribution of host-plant species within a habitat; variation in leafing phenology within and between species and individuals—and it is not difficult to see why being polyphagous is evolutionarily advantageous. Polyphagy allows this species to persist and thrive in an uncertain, heterogeneous environment—by decreasing specificity in one aspect of its niche, it is able to specialise on a narrow phenological niche.

Although the polyphagous habit is maintained throughout the distribution of the winter moth, we see indications that performance on particular host-plant species can be modulated in certain environments and populations, perhaps adjusting to increase fitness on locally abundant hosts, while still being able to persist on almost whatever plant material is available—a great advantage in a variable environment where host-choice by females is limited. The evidence presented here, and in the literature, suggests that throughout its range there are many plant species acceptable to winter moth caterpillars, on which performance is at least comparable to oak. This ability to effectively utilise a very large range of host-plant species might ameliorate the negative effects of phenological asynchrony with bud-burst on any one host-plant species—even if selection for synchrony is uniformly strong across all host-plant species and individuals, a phenologically variable winter moth population, with caterpillars hatching randomly across a subset of host-plants, would perhaps on average perform better than if it were specialised on one host-plant only. Withstanding fluctuations and uncertainties in the environment might also have wider implications for the stability and robustness of the food webs and ecosystems of which this very abundant species forms a central part. This inherent resilience to an uncertain niche, and asynchrony with any one particular host-plant, might help buffer winter moth populations against future climatic changes affecting phenology (across all trophic levels in this system). For this reason it is critically important that we understand and consider the whole ecological context of a species before we can expect, with any confidence, to make projections as to the effects of climatic or environmental changes on their populations, or on those of species with which they interact.

Chapter 3: When does mismatch matter? A multi-species analysis of the fitness impacts of tree/caterpillar asynchrony

3.1. Abstract

Consumers that depend on a temporally ephemeral resource can suffer negative fitness consequences if their phenology is mistimed with respect to that of the resource—so-called *trophic mismatch*. Spring-feeding woodland caterpillars have become a standard study system for investigating this phenomenon. In general it is thought that fitness is maximised for caterpillars that hatch synchronously with young and highly palatable host-plant foliage, and declines with increasing asynchrony: hatch too early when buds have not burst and they may starve, hatch too late and host-plant palatability is greatly reduced. However, the phenological sensitivity to temperature can differ between caterpillars and their host-plants, and therefore climate change could potentially generate greater asynchrony. Much of the previous work on this system, however, focuses on a single caterpillar/host-plant species pairing—the winter moth *Operophtera brumata* and English oak *Quercus robur*. The extent to which we can generalise from this single interaction to other spring-feeding caterpillar species is unclear, and the effects of mismatch need not be equivalent across host-plant and caterpillar species. As such, these communities may be buffered at the population level against some degree of climate change induced temporal asynchrony with their host-plants. Here, in an experimental assay of nearly 18000 individuals, I tested the fitness effects of late-hatching asynchrony in six spring-feeding caterpillar species, across eight host-plant species. In contrast to many previous studies, I found that, while hatch/bud-break synchrony is important for fitness, timing matters within fairly broad bounds, at a scale of weeks and months, not days. Caterpillars are generally able to tolerate a substantial degree of asynchrony, although fitness does decline. The effects of asynchrony are, however, highly contingent on the particular caterpillar and host-plant species pairing involved—in some pairings asynchrony has little or no effect. Furthermore, not only are winter moths one of the species more strongly affected by asynchrony, oak is one of the host-plants on which caterpillar performance is generally poorest over time. Focusing on these particular taxa may be misleading if we generalise and infer the effects of asynchrony more broadly on the caterpillar guild. Many other systems, which we assume to be vulnerable to increased

mismatch as a result of climate warming, may have similar in-built buffering mechanisms and be more resilient than previously thought.

3.2. Introduction

The Earth's climate is changing, and these changes are expected to continue (IPCC, 2021). Advances in spring phenology across temperate species are one of the most conspicuous and heavily documented effects of recent increases in mean global temperature (Thackeray *et al.*, 2016; Cohen *et al.*, 2018; Roslin *et al.*, 2021). For species which depend on phenological synchrony with other species—that is, timing a particular event or stage in their life history so as to coincide with an event or stage in the life history of another species—such changes could be particularly consequential. Indeed, taxa at different trophic levels often show divergent phenological sensitivity to temperature changes (Thackeray *et al.*, 2016; Roslin *et al.*, 2021). In such circumstances, consumers relying on a temporally ephemeral resource taxon, for example, might find themselves mistimed with respect to its occurrence (van Asch and Visser, 2007; Both *et al.*, 2009; Burgess *et al.*, 2018). Differences in phenological sensitivity to temperature could result in plants finding their flowering phenology becoming increasingly asynchronous with the occurrence of their pollinators (Iler *et al.*, 2013). This concept has been formalised as the match-mismatch hypothesis (MMH) (Cushing, 1990; Durant *et al.*, 2007). First developed to explain differences in inter-annual recruitment to fish populations through the degree of synchrony with plankton production (Hjort, 1914; Cushing, 1967, 1969, 1975, 1990), it has come to be applied much more broadly to describe the detrimental fitness effects associated with phenological asynchrony between any two interacting species, most typically a consumer and its food source (Samplonius *et al.*, 2020).

Although the MMH is often invoked, evidence purporting to demonstrate the fitness effects of mismatch in the field is often incomplete (Samplonius *et al.*, 2020). In particular, the widespread tri-trophic tree/caterpillar/bird food-chain of temperate woodlands has become a standard terrestrial study system in which the MMH is conceptualised and tested. With the flush of fresh, young foliage on trees in spring, phytophagous caterpillars are suddenly provided with a new resource to exploit, if they can time their life history to match its availability. Caterpillar fitness seems to be closely linked to the degree of synchrony between egg hatch and host bud-burst (Wint, 1983; Kirsten and Topp, 1991; Watt and McFarlane, 1991; Dongen *et al.*, 1997; Tikkanen and Julkunen-Tiitto, 2003; van Asch *et al.*, 2007). Caterpillars which hatch too early find themselves without food and can starve (Thomson, 1954; Cuming, 1961; Patocka, 1972; Wint, 1983; Hunter, 1990; Tikkanen and Julkunen-Tiitto, 2003; van Asch *et al.*, 2007). Those which hatch too late are forced to feed on older, more mature foliage which is tougher (Feeny, 1970; Hunter, 1991; Haukioja *et al.*, 2002; Falk *et al.*, 2018; Fuentealba *et al.*, 2018), contains greater quantities of noxious secondary chemicals, such as tannins, and has reduced nutritional quality (Feeny, 1968, 1970; Schroeder, 1986; Hunter, 1991; Quiring, 1992; Dury *et al.*, 1998; Haukioja *et al.*, 2002; Tikkanen and Julkunen-Tiitto, 2003; Falk *et al.*, 2018). Selection, therefore, seems to act to promote the close synchrony of caterpillar and host phenology. In the caterpillars of the winter moth *Operophtera brumata*, for example, van Asch and Visser (2007) estimated that that hatching as little as five days before or after bud-burst on oak would reduce fitness almost to zero, relative to hatching in perfect synchrony. In the gypsy moth *Lymantria dispar*, Raupp *et al.* (1988) found that caterpillar survival to pupation declined significantly with increasing asynchrony after host bud-burst, reaching near zero after two weeks. Similar patterns can be observed in species feeding on non-deciduous trees—in the western spruce budworm *Choristoneura occidentalis*, survival is considerably lower on growth produced in previous years than on new foliage (Dodds *et al.*, 1996). Consistent with these data indicating strong selective pressures for local synchrony, van Dongen *et al*. (1997) found that the mean date of egg hatch of caterpillars on an individual host tree was positively correlated with the bud-burst phenology of that tree (R^2 ranged from 0.14 to 0.32 at different sites, within a year).

The timing of caterpillar eclosion and the timing of bud-break on deciduous trees is largely determined by two abiotic environmental factors: photoperiod (Tauber *et al.*, 1986; Basler and Körner, 2012) and temperature (Holliday, 1985; Tauber *et al.*, 1986; Buse and Good, 1996; Buse *et al.*, 1999; Marchin *et al.*, 2015; Lenz *et al.*, 2016). The rate of development of both trophic levels can generally be described well by a growing degree day model (Tauber *et al.*, 1986; Salk, 2011; Hibbard and Elkinton, 2015; Salis *et al.*, 2016), with both thermal sum and winter chilling (Visser and Holleman, 2001; Hibbard and Elkinton, 2015) exerting an influence on their respective timings. Despite the apparently strong selection for synchrony (Tikkanen and Julkunen-Tiitto, 2003; van Asch and Visser, 2007), however, the phenological sensitivity to temperature of these two trophic levels is seemingly unequal. Both in the field (Visser *et al.*, 2006; Both *et al.*, 2009; van Asch *et al.*, 2012; Burgess *et al.*, 2018) and in controlled experiments (Buse and Good, 1996; Sarfraz *et al.*, 2013; Schwartzberg *et al.*, 2014; Uelmen *et al.*, 2016; Ren *et al.*, 2020; Bellemin-Noël *et al.*, 2021), spring caterpillar phenology frequently responds to climate warming by advancing to a greater or lesser extent than the timing of bud-burst on their host-plants. For example, Visser and Holleman (2001) estimated using a hindcasting modelling approach that increases in temperature between 1975 and 2000 had caused winter moth populations in the Netherlands to become increasingly asynchronous with bud-burst on oak, because they seemed to respond to higher temperatures by advancing their phenology to a greater extent than did their host trees.

Although the trophic interaction between arboreal caterpillars and broadleaf trees encompasses many species at both trophic levels (Maitland Emmet and Heath, 1992; Robinson *et al.*, 2010; Langmaid *et al.*, 2018), the vast majority of our insights have focused on one specific caterpillar species—the winter moth—and often on one single primary producer—the English oak *Quercus robur* (see Chapter 2, esp. Table 2.2).

The winter moth is a small geometrid species that occurs widely in Holarctic, but is native to the Palaearctic. The adults are active in the coldest months of the year, though timings vary by location (see Kozhanchikov, 1950; Holliday, 1985; Cao and Luciano, 2004; Rubtsov and Utkina, 2011; Waring *et al.*, 2017), when, after mating, the flightless females ascend the trunks of trees and deposit their eggs. The caterpillars hatch over a period of several weeks (Speyer, 1938; Watt and McFarlane, 1991; Buse and Good, 1996; Ivashov *et al.*, 2002) in spring as the foliage begins to appear, in the characteristic pattern shown by many other spring-feeding caterpillars. Winter moth populations typically undergo cyclical fluctuations in size (Embree, 1965; Varley *et al.*, 1974; Rubtsov and Utkina, 2011), which may be partly explained by the mean degree of synchrony with host-plant phenology at the population level (Varley *et al.*, 1974). The winter moth has become a standard model species in the study of the MMH (van Asch and Visser, 2007), and is frequently taken as representative of the other members of the spring-feeding caterpillar guild. However, though winter moths are often the dominant caterpillar species in spring deciduous woodlands by a large margin (Feeny, 1970; Shutt *et al.*, 2019a), other species do occur at significant levels and sometimes exceed it in abundance—for example, Kulfan *et al.* (2018) found that in a Slovakian forest in spring, the caterpillars of the spring usher moth *Agriopis leucophaearia* comprised 70-80% of individuals beaten from *Quercus* foliage. Hitherto, our understanding of how the phenology of other species will be effected by climate change and the impact this will have on synchrony with their host-plants is very limited (van Asch and Visser, 2007)—crucially, the extent to which we can generalise from the winter moth to these other species is unclear.

Despite most spring-feeding caterpillar species being considerably polyphagous (Maitland Emmet and Heath, 1992; Porter, 2010; Waring *et al.*, 2017; Henwood *et al.*, 2020), there has been an almost exclusive focus in literature on synchrony and the MMH on single moth/host-plant species pairings (van Asch and Visser, 2007) (e.g. Table 2.2). In the winter moth, the role of oak is emphasised, particularly the English oak *Quercus robur* (a focus likely originating with Feeny, 1970). In fact, winter moth caterpillars have been recorded feeding in the field on plants from 31 different genera across 15 families, on species as taxonomically and morphologically diverse as birch, heather, and bilberry (Robinson *et al.*, 2010) (see Chapter 2). Of the thirteen studies which examine the effects of timing on various aspects of fitness or performance of winter moth caterpillars, only two consider more than two host-plant species, and the majority consider only *Quercus robur* (Table 3.1). The polyphagous habit of most spring-feeding caterpillars is important because not only will different host-plants vary in their inherent palatability to different caterpillar species (e.g. Chapter 2), they also differ in their underlying phenology (Crawley and Akhteruzzaman, 1988; Kramer, 1995; Wielgolaski, 2001; Karlsen *et al.*, 2007; Basler and Körner, 2012; Geng *et al.*, 2020; Gaytán *et al.*, 2022) and in the processes and rates of leaf maturation—the biochemical and structural changes that occur as leaves open, grow, and age on trees of different species, and even different individual trees, will be distinct (Feeny, 1970; Schroeder, 1986; Ruuhola *et al.*, 2001; Tikkanen and Julkunen-Tiitto, 2003; Forkner *et al.*, 2004; Laitinen *et al.*, 2005)—such that the fitness effects of asynchrony on each has the potential to be very different. For example, for the caterpillars of the winter moth the fitness costs of hatching asynchronously appear to be lower, or non-existent, on heather *Calluna vulgaris* (Kerslake and Hartley, 1997) and Sitka spruce *Picea sitchensis* (Hunter *et al.*, 1991) compared with oak (van Asch *et al.*, 2007). Leaf aging, and therefore asynchrony, need not have equivalent negative effects for all species of caterpillars on different host-plant species.

Table 3.1. The effects of asynchrony on fitness in the winter moth *Operophtera brumata*: a summary of the literature. Country describes where the experiment was carried out. Performance Metrics used are: S (survival); P (pupal mass); GR (growth rate); DI (development index); DT (development time); FAb (abundance across host-plants measured in the field); LP (larval choice experiment); F (fecundity).

Paper	Country	Host-plant Species	Performance Metrics	Summary of Findings
Feeny (1970)	UK	*Quercus robur*	P	Fourth instar caterpillars were fed on frozen foliage of different ages (“young” leaves, collected in the field on 16 May, and “mature” leaves collected on 28 May). Caterpillars fed on mature foliage produced pupae which were significantly smaller than those fed on young leaves (~10 mg vs ~30mg). Feeding caterpillars on an artificial agar diet made from ground leaf powder of both age categories did not produce a significant difference in pupal mass. It is argued that this difference is at least in part attributed to increased leaf toughness as they age.
Wint (1983)	UK	*Malus sylvestris* *Prunus spinose* *Crataegus monogyna* *Fagus sylvatica* *Corylus avellana* *Quercus robur*	S, P, DT, LP	Eggs were hatched in captivity in each of three months (May, June, July) and caterpillars reared in a lab environment in small groups at a constant 20°C. Survival is among its lowest (~30%) on oak, and lower only on beech *Fagus sylvatica* or mature hawthorn. Development time is shortest on oak while pupal mass is higher than on almost all other host-plant species. Across time there are generally substantial (and often significant) increases in mortality, development times, and declines in pupal mass, in every host-plant species, although there is also considerable stochastic variation between years and synchrony treatment groups, perhaps due to small within treatment sample size (e.g. mean pupal mass on oak in the May trial was 42.16mg in 1976 and 31.95mg in 1977).

cont.

Watt and McFarlane (1991)	UK	*Picea sitchensis*	S	On Sitka spruce *Picea sitchensis*, larval survival declines over the course of several months as new shoots grow larger and mature. From 18 Apr to 13 Jun survival declines from ~60% to near zero, at an initially slow, then accelerating rate.
Hunter *et al.* (1991)	UK	*Picea sitchensis*	P	There was no significant difference in the timing of bud-burst at sites which had very different levels of abundance of winter moth caterpillars. The authors suggest that synchrony is not as important for fitness on Sitka spruce as on oak.
Kirsten and Topp (1991)	Germany	*Quercus robur* *Salix alba alba* *Salix alba vitelline* *Salix x rubens* *Salix fragilis* *Salix viminalis* *Salix caprea* *Salix triandra*	P, GR, F	Growth rate of late instar caterpillars in *Salix* x *rubens* and *Salix fragilis* declines with increasingly late caterpillar hatch. On these two host-plants, hatching 30 days later results in a reduction in growth rate by approximately two thirds.
Kerslake and Hartley (1997)	UK	*Calluna vulgaris*	S, P, GR, DI	Livestock derived from an oak-feeding and a heather-feeding population were both reared on heather. The timing of larval eclosion (hence, the degree of synchrony with growth on the heather) was delayed by 30 days in one treatment group. Caterpillar survival is much greater in individuals derived from heather-feeding populations, relative to oak-feeding populations (~40% vs ~10%). There was no significant difference in survival or pupal mass between delayed (heather = 23.7, oak = 21.05mg) and undelayed (heather = 24.08, oak = 24.52mg) treatment groups. Growth rate of caterpillars, however, is significantly slower on the delayed treatment groups.

cont.

Dongen *et al.* (1997)	Belgium	*Quercus robur*	F	Sampled across several sites over a five year period. Host tree bud-burst date and caterpillar hatch date were significantly correlated (R^2 reaching a maximum of ~30%, much less in most sites). The correlation coefficient between bud-burst and hatch date at each site was itself significantly correlated with adult female winter moth size at that site in winter. Sites with a greater degree of correlation between bud-burst and caterpillar hatch produced larger, and likely therefore more fecund (see Appendix 2), females. Suggests selection favours synchronous hatching with bud-burst on the host tree.
Buse *et al.* (1999)	UK	*Quercus robur*	P	In an experimental set-up, caterpillars and their host trees were subjected to an artificial temperature increase of 3°C or maintained at ambient levels. Caterpillars maintained at 15°C but fed on elevated temperature leaves produced pupae which were lighter than those fed on ambient temperature leaves (38·6 and 42·9 mg). However, there was no significant difference in pupal mass when caterpillars (either ambient or elevated temperature treatments) were fed on leaves grown under the same temperature treatment as themselves (28·0 and 27·5 mg). This suggests elevated environmental temperature affects neither the degree of synchrony nor the ability of larvae to consume leaves which trees produce under those conditions.
Tikkanen and Lyytikäinen-Saarenmaa (2002)	Finland; Denmark	*Prunus padus* *Quercus robur*	P, GR, DT	As caterpillars hatched later—increasingly asynchronous with bud-burst—pupal mass declined significantly and development time increased significantly, across both host-plant species. Growth rate declined with increasing asynchrony, but did so at a greater rate on oak than on cherry.

cont.

Tikkanen and Julkunen-Tiitto (2003)(Van Dongen, 2006)	UK	*Quercus robur*	S, F	Both survival and the fecundity of adult females decreased significantly with increasing asynchrony. Caterpillar mortality before pupation reached 100% when caterpillars hatched ~100 degree days (DD) asynchronously. From this, and estimates of the reduction in fitness resulting from early hatching, they estimate a (asymmetric) fitness profile for caterpillar phenology, which peaks at perfect synchrony with host-plant bud-burst, and declines to zero 100dd after synchrony and 40dd before. [Degree days were estimates with a 5°C threshold. Thus, 100dd would be 20 days at 10°C (dd added each day = temp – threshold)]
Van Dongen (2006)	Belgium	*Quercus robur*	P	Identified freshly flushed oak leaves or one week old foliage. Caterpillars fed the older foliage were on average 3.13mg lighter (CIs: 5.46, 0.77). This would result in a reduction in adult female fecundity (see Appendix 2).
van Asch *et al.* (2007)	Netherlands	*Quercus robur*	S, P	Caterpillars were hatched concurrently and fed on foliage from three neighbouring trees on which buds burst at different times, such that there were three treatment groups—five days early, synchronous, and five days late. Early hatching caterpillars have low survival, but those which survive until bud-burst feed on foliage at its peak palatability and so produce large pupae, and therefore adults with high fecundity. Caterpillars hatching later have higher survival but feed on less palatable leaves and therefore have lower adult fecundity. This has the effect of producing an almost symmetrical fitness profile in which perfect synchrony is optimal. The relative fitness of caterpillars hatching as little as five days late or early is estimated to decline to near zero.

cont.

Wesołowski and Rowiński (2008)	Poland	*Quercus robur*	FAb	Frass-fall (a proxy for caterpillar abundance) and defoliation were significantly greater on early-flushing than late-flushing oak *Q. robur* trees. This suggests that the negative effects of asynchrony on the late flushing trees limit caterpillar numbers on them. Late bud-burst can be thought of as an anti-herbivory defence.
Kulfan *et al.* (2018)	Slovakia	*Quercus cerris* *Quercus pubescens*	FAb	Bud-burst on *Q. cerris* is later than that of *Q. pubescens*. Winter moth caterpillars are less abundant on the later flushing species than on the early flushing one (approx. 5% vs 10%). The authors argue this is a consequence of the negative effects of asynchrony on the former—caterpillars hatch too early on the late flushing species and die of starvation.

Table 3.1 cont.

In contrast to the simplified host-plant/caterpillar interactions we find described in the literature, then, we might expect instead to see in nature a complex set of interconnected and variable fitness responses across time shown by different caterpillar species. Across the caterpillar guild, only some species will find themselves asynchronous with some host-plant species, because of variation in the phenological sensitivity of the caterpillars (and their host-plants) to temperature. At an individual level, a broadly polyphagous diet and variation in the degree to which host-plant tissue becomes unpalatable with age might allow caterpillars to cope with a certain, limited amount of asynchrony. On some host-plant species asynchrony may not lead to appreciable mismatch, and some caterpillar species may possess adaptations or behavioural traits that make them more resilient to mismatch than others (see Chapter 4). This complexity could buffer caterpillars, at an individual and population level, against the uncertainty and unpredictability inherent in the spring-feeding niche and perhaps any future increases in the incidence of asynchrony induced by climate change.

In order to gauge the impact of ongoing climatic changes on temperate woodland communities and, by extension, other ecosystems in which phenological synchrony occurs, it is vitally important that we understand how spring-feeding caterpillar species more broadly are affected by trophic mismatch, and the extent to which we can generalise these effects across the guild. Here, I have attempted to directly address this limitation in our current knowledge. I quantified the performance effects (across several metrics) of hatching up to two months late in assays of six spring-feeding caterpillar species across eight host-plant species, using nearly 18000 individuals. I considered: *a*) the average effect of asynchrony on performance across all host-plant and caterpillar species; *b*) whether the average effects of asynchrony differed across host-plant species; *c*) whether the average effects of asynchrony differed across caterpillar species; and, *d*) to what extent the impacts of asynchrony were unique to specific host-plant and caterpillar species combinations. The average effect of asynchrony estimated in (*a*) gives some idea of the general cross-species impacts of hatching late, while the magnitude of the among species variation in the fitness consequences of asynchrony, estimated in (*b*)-(*d*), has implications for how far we can generalise on the basis of studying individual interactions and particular host-plant/caterpillar species pairings. If the winter moth is not particularly representative of other spring-feeding caterpillar species, for example, we might find that other species more generally are buffered against mismatch to a greater extent. Given the prominent treatment of the winter moth in the MMH literature and our greater understanding of how female pupal mass relates to fitness in this species, I give it special consideration and (*e*) additionally estimate the effects of asynchrony on a measure of absolute fitness.

3.3. Methods

3.3.1 Caterpillar species

I obtained livestock from six phytophagous, externally feeding British moth species, from two taxonomic families: the winter moth *Operophtera brumata*, the mottled umber *Erannis defoliaria* (both Geometridae); the gypsy moth *Lymantria dispar*, the black arches *Lymantria monacha*, the vapourer *Orgyia antiqua*, and the scarce vapourer *Orgyia recens* (all Erebidae) (Appendix 7). These species are generally widespread and common, and all have larvae which feed in early spring in Britain (Henwood *et al.*, 2020). All overwinter as ova except the scarce vapourer which passes this period as a diapausing first instar larva (Skinner, 2009; Porter, 2010).

Female winter moths were collected over two years (from 25 Nov 2019 to 8 Jan 2020 and 17 Nov 2020 to 27 Dec 2020) in the Hermitage of Braid LNR (Edinburgh) using lobster-pot style trunk traps, modelled on those described by (Varley *et al.*, 1974), which intercepted females as they ascended trees after eclosion (see Appendix 9). After collection females were placed individually in 75 x 25mm glass phials with a wad of cotton at the bottom to act as an egg laying medium. Females were stored at ~5°C in complete darkness and allowed to lay freely. Approximately one month later, all tubes were examined and the dead females were removed. Ova from a total of 126 females from the Edinburgh site were obtained in the winter of 2019, and from 85 females in the winter of 2020. Ova (or larvae, for the scarce vapourer) were obtained for the remaining species from entomologists or entomological supply companies across the United Kingdom. For each species, individuals were obtained from at least ten distinct, outbred broods. Most were sourced solely from a single population, though the source population differed between species (Appendix 1, Table S3.2).

3.3.2. Rearing methodology

Ova/larvae of all species were stored at 5°C (ranged from 4-7°C, using a Russell Hobbs RHCLRF17 tabletop refrigerator) to prevent early hatch or diapause break. As required for the experiment, ova were removed from cold storage and placed at room temperature (ranged from 17-21°C) to stimulate egg hatching. A subset of ova, sampled from across all broods, were removed concurrently and allowed to hatch. Exposure to relatively high temperatures helped ensure individuals hatched at the same time, despite inter- and intra-brood variation in the temperature requirements for eclosion. Larvae were assigned at random to each treatment group, and subsequently to each rearing culture within that treatment group.

Larvae were reared in groups of ten individuals (a "culture", see Figure 3.1), firstly in small 75 x 50 x 15mm transparent plastic containers and then, at around the third instar, into larger 175 x 100 x 50mm disposable plastic food containers (see Appendix 11). The rearing containers were lined with white absorbent paper towels. Freshly excised food was placed in each container and examined daily to check its condition and how much remained. Typically it was replaced daily, no less than every second day. Larvae were provided with an excess of plant material at all times such that the quantity of food was never a limiting factor to growth. The tissue lining of the container was replaced each time new food was provided. At the completion of their development larvae pupated in the tissue at the base of the container. After all larvae had pupated, excess host-plant material was removed and the containers were stored at room temperature. One month after pupation, pupae were removed, laid out on cotton for emergence, and stored outdoors under a canopy at ambient environmental temperature (56.06°N, -3.77°E).

3.3.3. Asynchrony assays across moth species and host-plants

In this experiment, I aimed to quantify the fitness effects of varying degrees of asynchrony across spring-feeding caterpillars on a range of host-plant species. I selected eight host-plant species which are common and widespread in Britain and which are known to be used by all of the caterpillars studied in the field (Robinson *et al.*, 2010) for use in the assays: alder *Alnus glutinosa*, apple *Malus domestica*, birch *Betula pendula*, hawthorn *Crataegus monogyna*, oak *Quercus robur*, sallow *Salix capraea*, sycamore *Acer pseudoplatanus*, and willow *Salix alba* (Appendix 7).

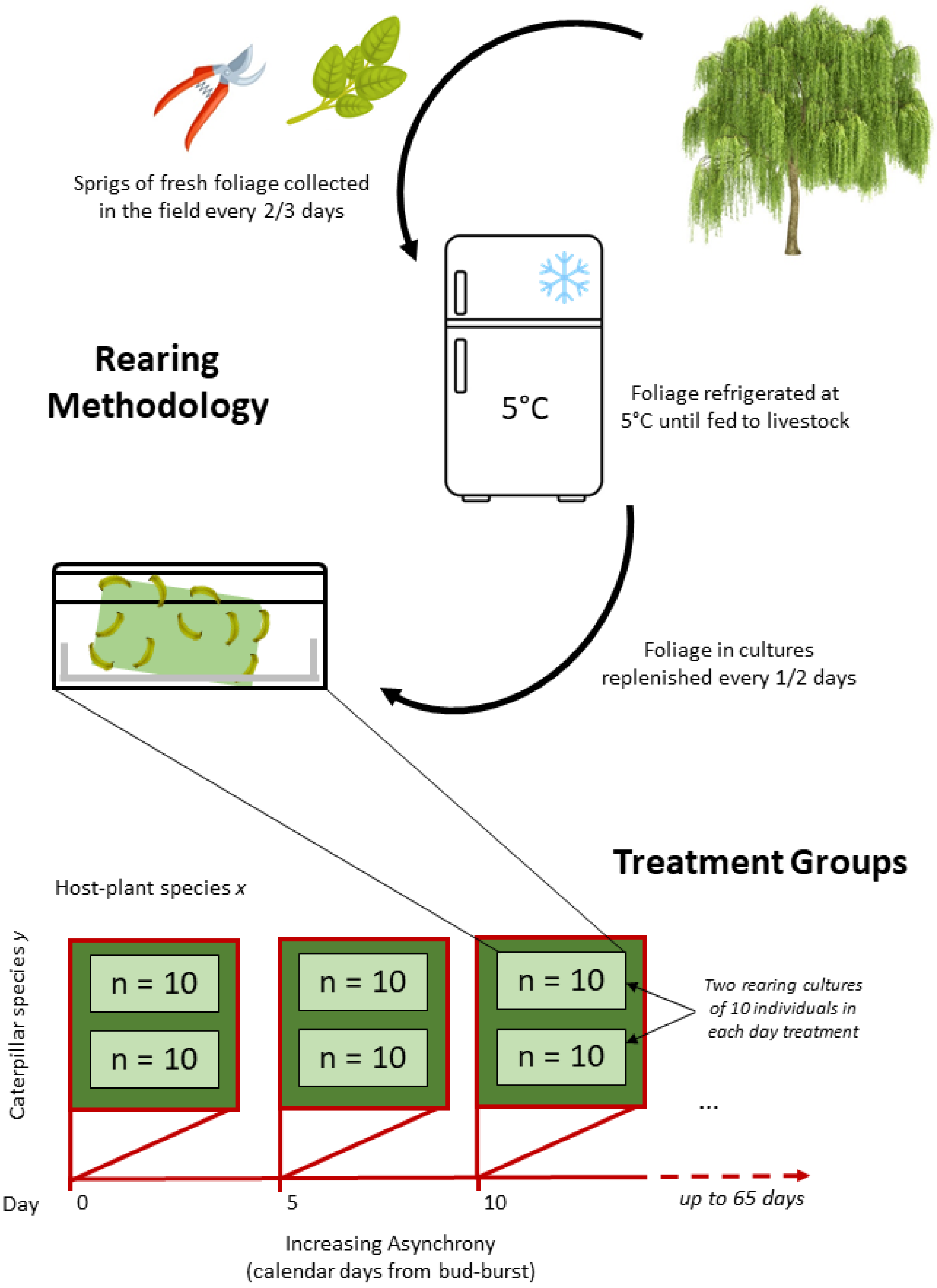


Figure 3.1. Schematic of experimental design for Chapter 3. Livestock from six spring-feeding caterpillar species were reared to pupation on foliage from eight different host-plant species. The hatching time of caterpillars was manipulated so as to simulate various degrees of asynchrony relative to host bud-burst. Caterpillars were reared in cultures of 10 individuals. Performance in each host by population treatment was quantified on three metrics: survival to pupation, final pupal mass, and development time.

Increasing larval asynchrony with the host-plant was simulated by staggering hatching date while the foliage naturally aged in the field. The experiment was begun for each plant species when a sufficient number of individual trees could be sampled in the field at the “first full leaf” stage (i.e. Bud Stage 4, see Table 4.2)—this was taken as the date at which the first fully unfurled leaf with a recognisable shape was observed in the field and designated “Day 0”. Consequently, the experiment initiated on different calendar dates for each host-plant species, although these were co-ordinated so as to be as close together as possible, and generally did not differ by more than 5 days from one another (Appendix 1, Table S3.2). The experiment was conducted over two years and synchrony treatments differed slightly across years (see Appendix 1 Table S3.1). In 2020, it featured winter moth, mottled umber, and vapourer caterpillars on all host-plants, and in 2021 all caterpillar species on all host-plants.

Fresh foliage was collected from at least 12 individual trees of each species every two to three days (Figure 3.1). Cut sprigs 15cm in length were stored in airtight plastic bags at 5°C until required for feeding, to maintain freshness. Foliage was collected from trees near Falkirk (Stirlingshire; 56.069°N, -3.767°E) and Kincardine (Fife; 56.057°N, -3.613°E). Because hatching was staggered, all larvae active at any one time were fed on samples of the same foliage collection. The secondary chemistry of plant leaves can vary not only between species but also between individuals of the same species, due to local differences in environmental conditions, soil chemistry, local geology, and associated plant species, for example (e.g. Laitinen *et al.*, 2005; Lindroth, 2012; Kos *et al.*, 2015). This variation could affect the fitness of insects feeding on those leaves. In order to minimise the effects of individual variation in leaf properties *within a species*, leaves from across all the sampled tree individuals were randomly assigned to each rearing culture, such that larvae at any one time had access to foliage from a range of different host-plant individuals of the same species. This reduced the likelihood of a single poor host-plant individual markedly affecting any particular rearing culture.

The performance of caterpillars in each treatment group was quantified by measuring: the survival of each individual from hatch to pupation; the final pupal mass attained in mg by each individual one month after pupation (a widely used, robust, and accurate predictor of future female fecundity, see Appendix 2; quantified using a Mettler AJ50 balance); and, the development time in days from hatch to pupation (a longer developmental period potentially exposes caterpillars to increased predation, parasitism, and exposure to adverse environmental conditions). Since larvae were reared in groups it was not possible to relate each of these values to a specific individual.

3.3.4. Statistical analysis

I fitted generalised linear mixed models to the data in *R* v. 4.0.3 using the Bayesian package MCMCglmm (Hadfield, 2010). Survival to pupation (binomial), pupal mass (Gaussian), and development time (Gaussian) were each modelled separately. Model structure was similar across each of these three performance metrics, although sex was fitted for mass and development time (Table 3.2)—sex could not be determined for caterpillars before pupation. Models were designed *a priori* and not simplified. Whilst sex and sex by host-plant and caterpillar species interaction effects add to the model complexity, they were included because of the extent of observed variation in the raw data between the two sexes. For example, not only are there considerable differences in the size of pupae across the different caterpillar species, the difference in size between male and female pupae also varies by species. To simplify the model, sex could have been omitted if survival was equivalent across time—in such circumstances, the sex-based differences would balance each other out. There are good reasons for thinking this is not the case, however. For example, females, tending to be larger, are often more robust and usually show higher survival under a range of stressful conditions. Furthermore, in many cases it is the response of females that may be most relevant to studying fitness—with respect to pupal mass, this relates to fecundity clearly in female individuals (see Appendix 2). The effects of mass on male fitness are largely unknown. Where analyses used a reference level, this was specified as the females, and all figures shown here which do not specify otherwise show strictly the female responses.

Models were run for 1.5 million iterations, with thinning every 100 iterations and a burn-in of 500000. Bayesian models used the default priors on the fixed effects (mean = 0, with a large variance), inverse Wishart priors on the residual (though for the binary survival models the residual was fixed), and parameter expanded priors for the random effects. Previous studies suggest we might expect a quadratic relationship between performance and degree of asynchrony (Tikkanen and Julkunen-Tiitto, 2003; van Asch *et al.*, 2007), so I inspected the model fits against the raw data, and found that in this case a simple linear model fit the data

Table 3.2. Model structures giving a justification of each term. Models of mass and development time had identical structures. For between Year and Sex comparisons, 2020 and females are taken as the reference level, respectively. Some of these terms (e.g. Sex, Year, and Culture) were included to increase the fit of the model to the data, but the outputs are not discussed at length because they are not relevant to the specific hypotheses considered here:

a) what is the average effect of asynchrony on fitness across all host-plant and caterpillar species?;

b) do the average effects of asynchrony differ across host-plant species?;

c) do the average effects of asynchrony differ across caterpillar species?;

d) to what extent are the impacts of asynchrony unique to specific host-plant and caterpillar species combinations?

Random terms estimate variance across the different random effects (i.e. levels of that factor). The relative magnitude of estimates of the variance in the slopes of each random effect and interaction indicates the relative importance of each, and their impact on the fitness effects of asynchrony. Three way interactions, such as Day : Host : Species, indicate an idiosyncratic effect of host-plant on performance (i.e. survival, mass, development time) in each caterpillar species. ^ indicates as for survival model.

Model		**Effect/Interaction**	**Rand. Slopes**	**Hypothesis Tested**	**Justification**
Survival	Fixed	Day		*a*	Slope of the average effects of increasing asynchrony
		Year			Effect of Year on the Day intercept (2021 vs 2020)
		Day : Year			Effect of Year on the Day slope (2021 vs 2020)
	Random	Culture			Effect of rearing culture on the Day intercept
		Host	Day	*b*	Effects of Host-plant species on the slope and intercept of Day
		Species	Day	*c*	Effects of caterpillar Species on the slope and intercept of Day
		Host : Species	Day	*d*	Differences in the effects of Host-plant species on slope and intercept of Day among caterpillar Species

cont.

		Year : Host : Species	Day		Differences in the effects of Host-plant species on slope and intercept of Day among caterpillar Species between Years
Mass / Dev Time	Fixed	Day		*a*	^
		Sex			Effects of Sex on the Day intercept
		Year			^
		Day : Year			^
		Day : Sex			Effects of Sex on the Day slope
	Random	Culture			^
		Host	Day	*b*	^
		Species	Day	*c*	^
		Sex : Species	Day		Differences in the effects of caterpillar Species on slope and intercept of Day between Sexes
		Sex : Host	Day		Differences in the effects of Host-plant species on slope and intercept of Day between Sexes
		Species : Host	Day	*d*	^
		Sex : Species : Host	Day		Differences in the effects of caterpillar Species on slope and intercept of Day among Host-plant species between Sexes
		Year : Species : Host	Day		^

Table 3.2 cont.

well. I generated predictions of the performance effects of asynchrony (a) averaged across all host-plant and caterpillar species combinations; (b) on each host-plant species, averaged across all caterpillar species; (c) on each caterpillar species, averaged across all host-plant species; and (d) on each host-plant by caterpillar species combination. To estimate the variance accounted for by each of the random terms I estimated the mean and 95% HPD intervals. Model outputs are stated on the link scale (logit for survival, and Gaussian for mass and development times). To further assess the relative importance of host-plant, caterpillar species, and host-plant by caterpillar interactions on the effects of asynchrony, I used the posterior estimates of the variance of each term to estimate their relative explanatory contribution in each model. Given the significance of the winter moth as a study species in the literature, I used the posterior estimates of survival and pupal mass to estimate a measure of absolute fitness across each host-plant treatment group (for a detailed methodology, see Appendix 2).

3.4. Results

3.4.1. Performance effects across host-plant and caterpillar species

(a) What is the average effect of asynchrony on performance across all host-plant and caterpillar species?

As caterpillars hatched increasingly asynchronously with bud-burst in their host-plants there was a significant decrease in their probability of survival to pupation (slope = -0.06, 95% CIs: -0.08, -0.03) and a slight decrease in the final pupal mass the caterpillars attain (slope = -0.57, CIs: -1.40, 0.32) though the latter was not significant (Figure 3.2). The effect of increasing asynchrony on development time (slope = 0.06, CIs: -0.14, 0.27) was non-significant, meaning that caterpillars hatching later tend not to take significantly longer to reach pupation on average (Figure 3.2).

(b) Do the average effects of asynchrony differ across host-plant species?

In each of the three modelled metrics of performance, point estimates of the among host-plant variance in the intercept and slope of the effect of mismatch were quite substantial, but the lower credible intervals approach zero in all cases (Survival, intercept = 1.45, CIs: 0.00,

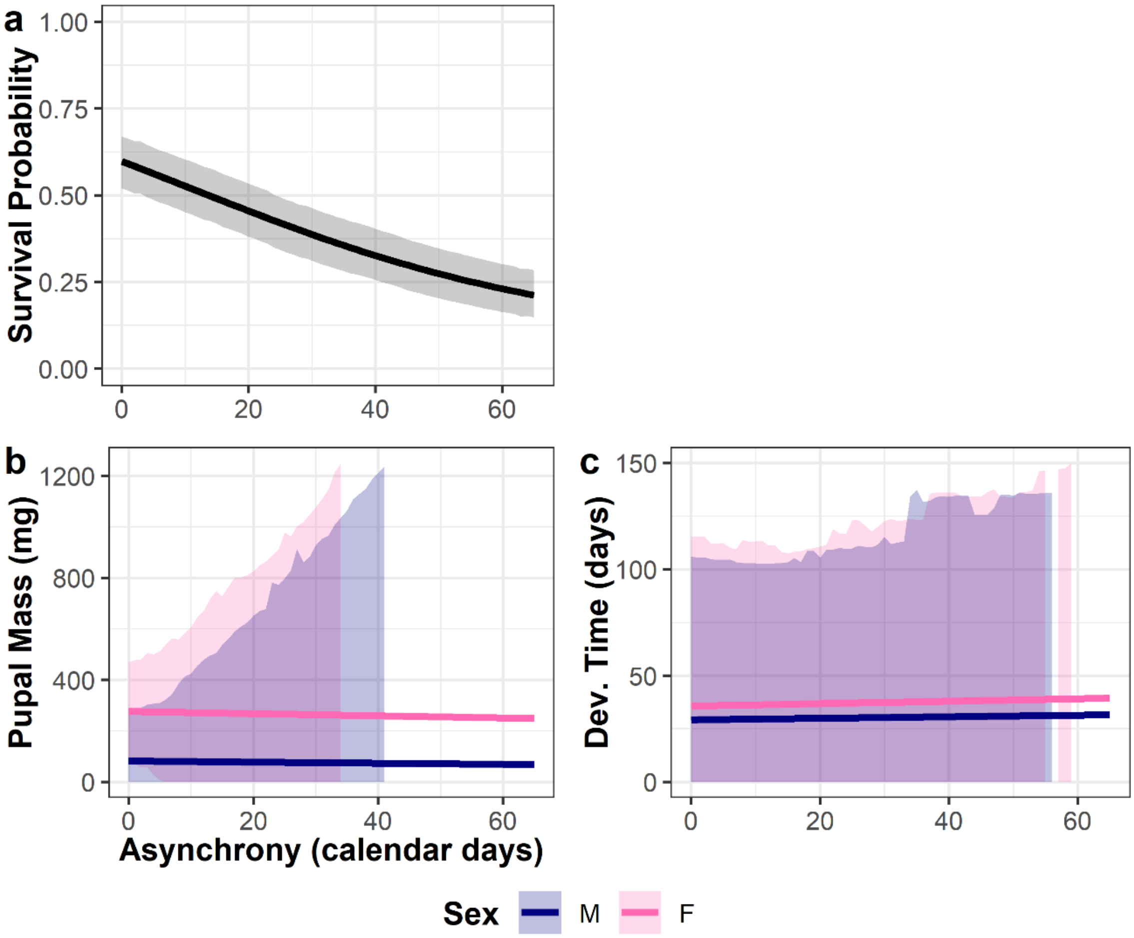


Figure 3.2. Overall modelled effects of asynchrony between caterpillar hatch and host bud-burst on three metrics of performance (± 95% CIs). Asynchrony represents the number of calendar days after bud-burst on which the caterpillars eclosed. Survival probability to pupation was quantified across both sexes.

4.11, slope = 0.00, CIs: 0.00, 0.00; Mass, intercept = 767.74, CIs: 0.00, 2478.96, slope = 0.10, CIs: 0.00, 0.41; Dev. Time, intercept = 5.72, CIs: 0.00, 21.10, slope = 0.00, CIs: 0.00, 0.01).

Generally, there were only slight differences in the trends evident on different host-plant species (Figure 3.3). In pupal mass we see a clearer trend towards decline with increasing asynchrony in sallow and apple than on other host species. In the case of development time, there was a gradual trend towards prolonged caterpillar development with increasing asynchrony on all species.

(c) Do the average effects of asynchrony differ across caterpillar species?

In each of the three modelled metrics of performance, point estimates of the among caterpillar species variance in the intercept and slope of the effect of mismatch were

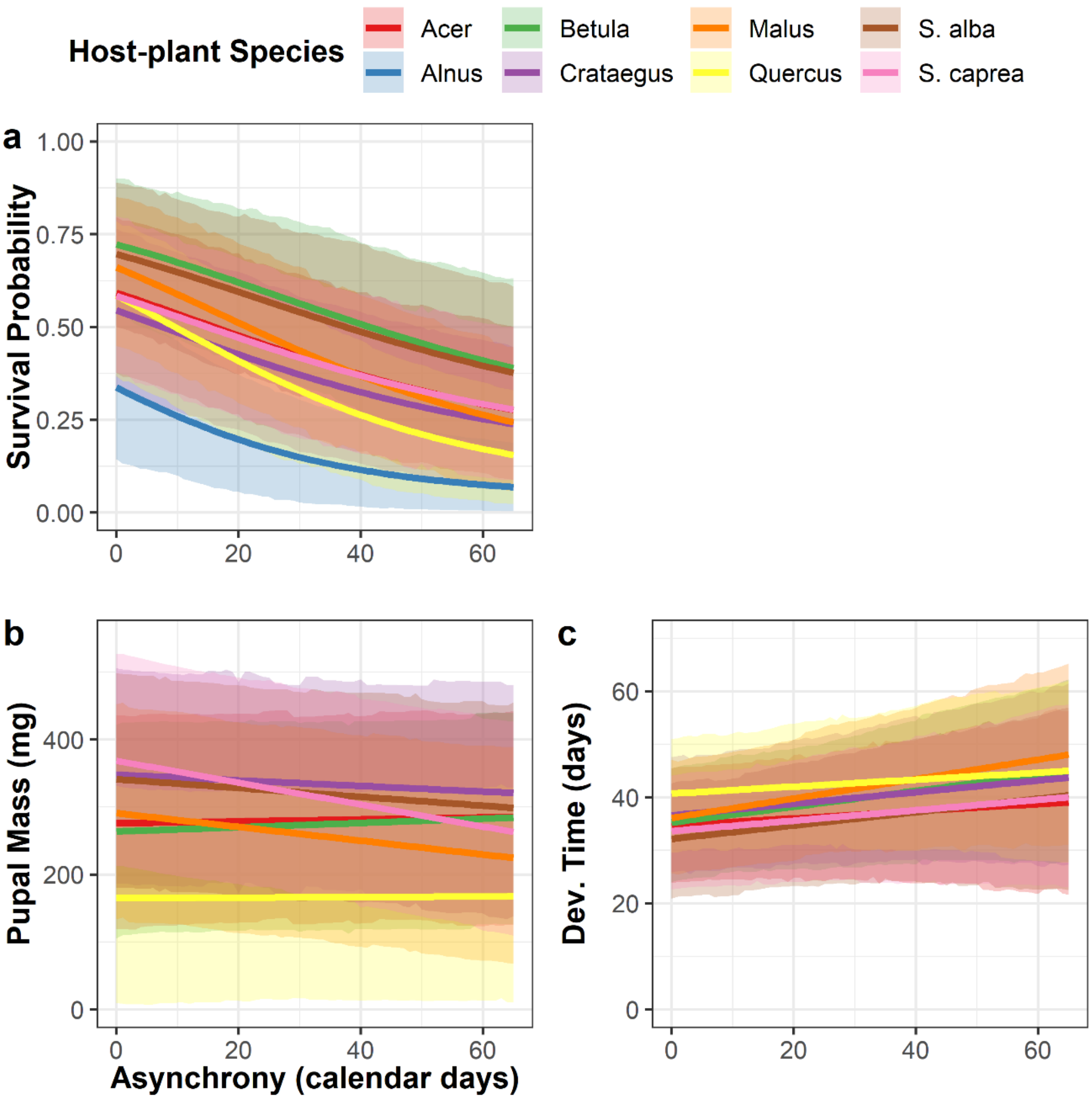


Figure 3.3. Divergent modelled effects of asynchrony between hatch and host bud-burst among host-plant species, on three metrics of performance (± 95% CIs). Asynchrony represents the number of calendar days after bud-burst on which the caterpillars eclosed. Survival probability to pupation was quantified across both sexes. Estimates for pupal mass and development time are shown for females only because they are most relevant in individuals of this sex.

substantial but the lower credible interval again generally approached zero (Survival, intercept = 2.47, CIs: 0.00, 7.49, slope = 0.00, CIs: 0.00, 0.00; Mass, intercept = 4965.85, CIs: 0.00, 20384.59, slope = 0.34, CIs: 0.00, 1.28; Dev. Time, intercept = 89.52, CIs: 0.00, 311.64, slope = 0.05, CIs: 0.00, 0.16).

The magnitude of the random slope variance estimates tended towards being greater than the among host-plant variance estimates, suggesting that caterpillar species may be a

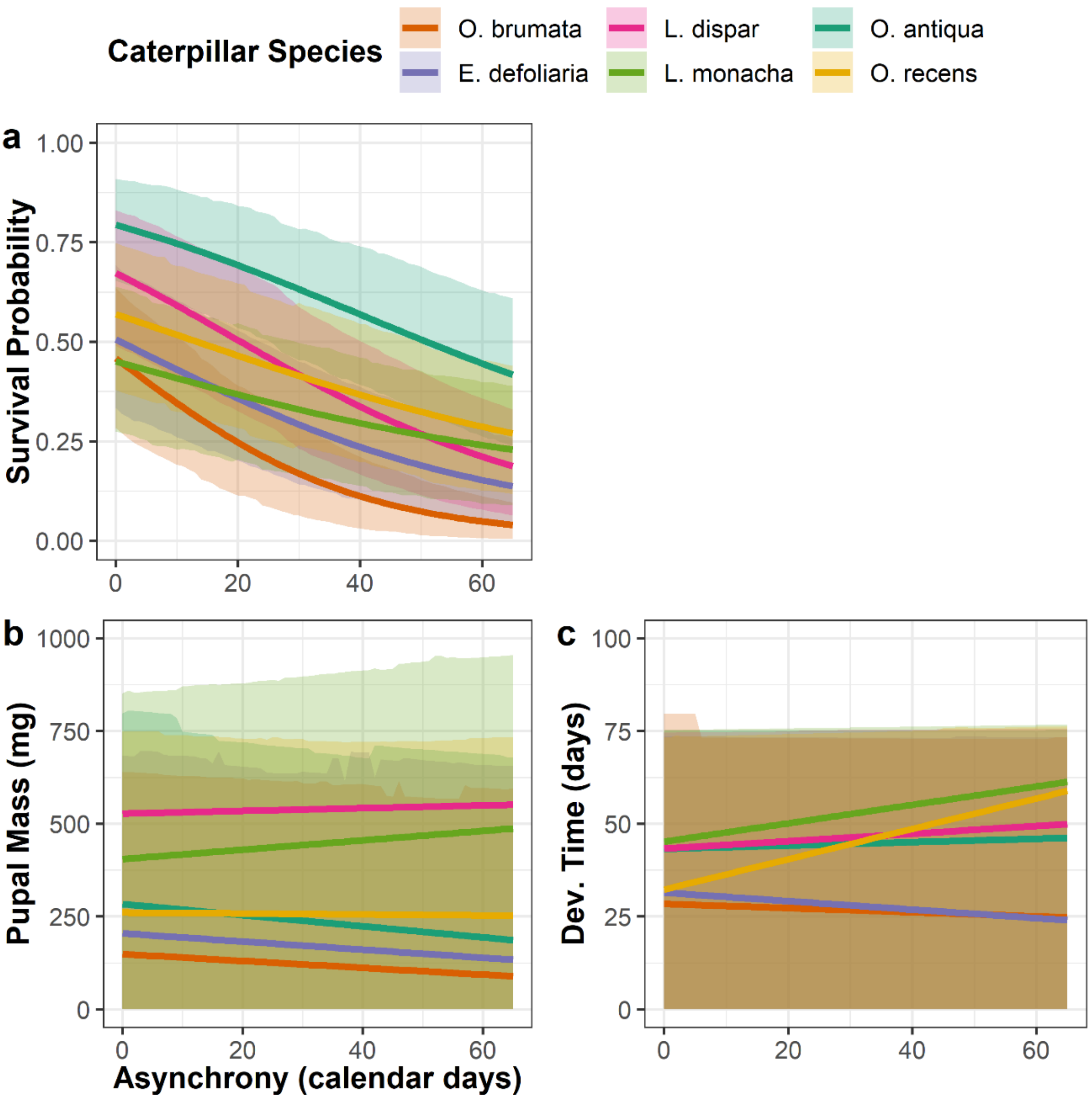


Figure 3.4. Divergent modelled effects of asynchrony between hatch and host bud-burst among caterpillar species, on three metrics of performance (± 95% CIs). Asynchrony represents the number of calendar days after bud-burst on which the caterpillars eclosed. Survival probability to pupation was quantified across both sexes. Estimates for pupal mass and development time are shown for females only because they are most relevant in individuals of this sex.

relatively more important determinant of the effects of asynchrony than is the plant on which individual caterpillars find themselves (Figure 3.4). I tested this apparent difference in slope variance formally by comparing HPD intervals, and found that while in all cases the differences are non-significant, it was close to significant in survival (95% CIs = -0.0005, 0.0026) and development time (95% CIs = -0.0032, 0.1576), but not pupal mass (95% CIs = -0.71, 1.43).

In survival, we can see no real discernible between-species differences in the effects of asynchrony (Figure 3.4). In the case of pupal mass, species showed a range of different but

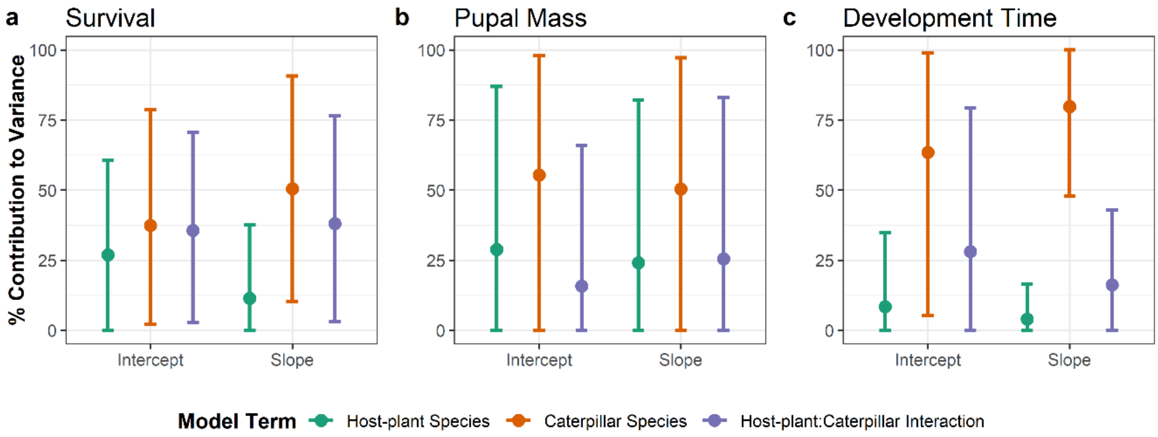


Figure 3.5. Relative percentage (mean ±95% CIs) contributions of host-plant species, caterpillar species, and host-plant by caterpillar interactions to variance in caterpillar survival, final pupal mass, and development time. Values shown are relative to the overall variance explained by all three terms in each model only, and not the total variance explained by the model overall.

subtle trends: declines in the vapourer, mottled umber, and winter moth; no difference in the scarce vapourer and gypsy moth; and increases in the black arches. The most marked differences were to be found in development time, where there are no real trends seen in most species with increasing asynchrony, but clear and steep increases in the scarce vapourer and black arches (Figure 3.4).

(d) To what extent are the impacts of asynchrony unique to specific host-plant and caterpillar species combinations?

There was a general tendency for significant variance in the intercept of the caterpillar and host-plant species interaction, though the lower credible interval tended towards zero in most cases (Survival, intercept = 1.53, CIs: 0.35, 2.81; Mass, intercept = 328.68, CIs: 0.00, 1110.51; Dev. Time, intercept = 15.62, CIs: 0.00, 5.53). This suggests that where synchrony was perfect (i.e. day = 0), performance on any particular host-plant species varied by caterpillar species, and vice versa. However, there was less substantial and no significant variance among *slopes* (Survival, slope = 0.00, CIs: 0.00, 0.01; Mass, slope = 0.09, CIs: 0.00, 0.32; Dev. Time, slope = 0.00, CIs: 0.00, 0.01). In spite of the fact that I often found superficially very different effects of asynchrony in different host-plant by caterpillar combinations (e.g. Figure 3.6), this suggests that there is no strong statistical support for this idea on average (Figure 3.5). Trends in pupal mass (Figure 3.7) and development time (Figure 3.8) are generally more consistent among these combinations than those of survival probability (Figure 3.6)—

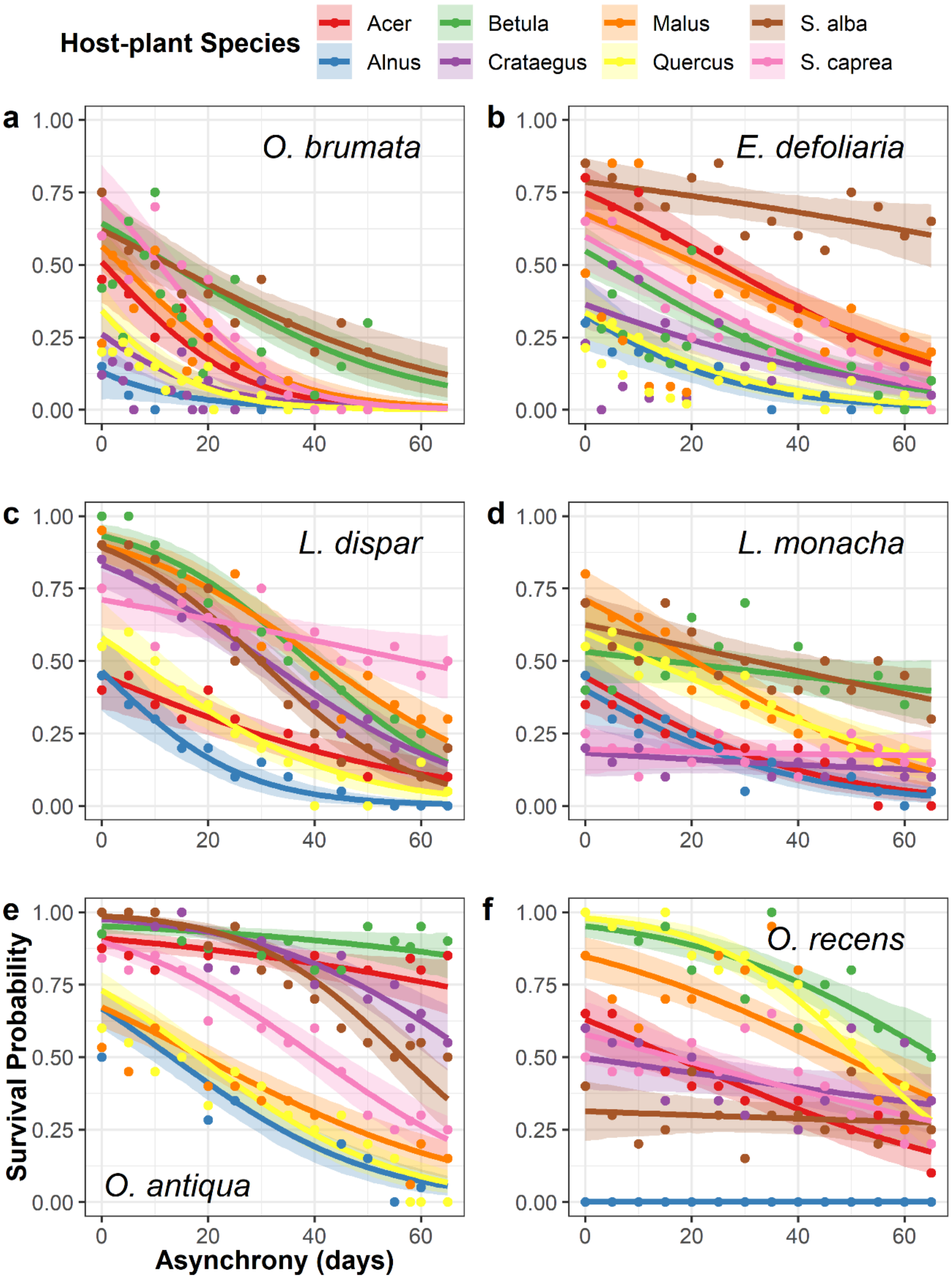


Figure 3.6. Modelled effects of asynchrony between hatch and host bud-burst on survival to pupation among caterpillar species (*a* - *f*), across eight host-plant species (± 95% CIs). Points show means of raw data. Asynchrony represents the number of calendar days after bud-burst on which the caterpillars eclosed. Survival probability to pupation was quantified across both sexes.

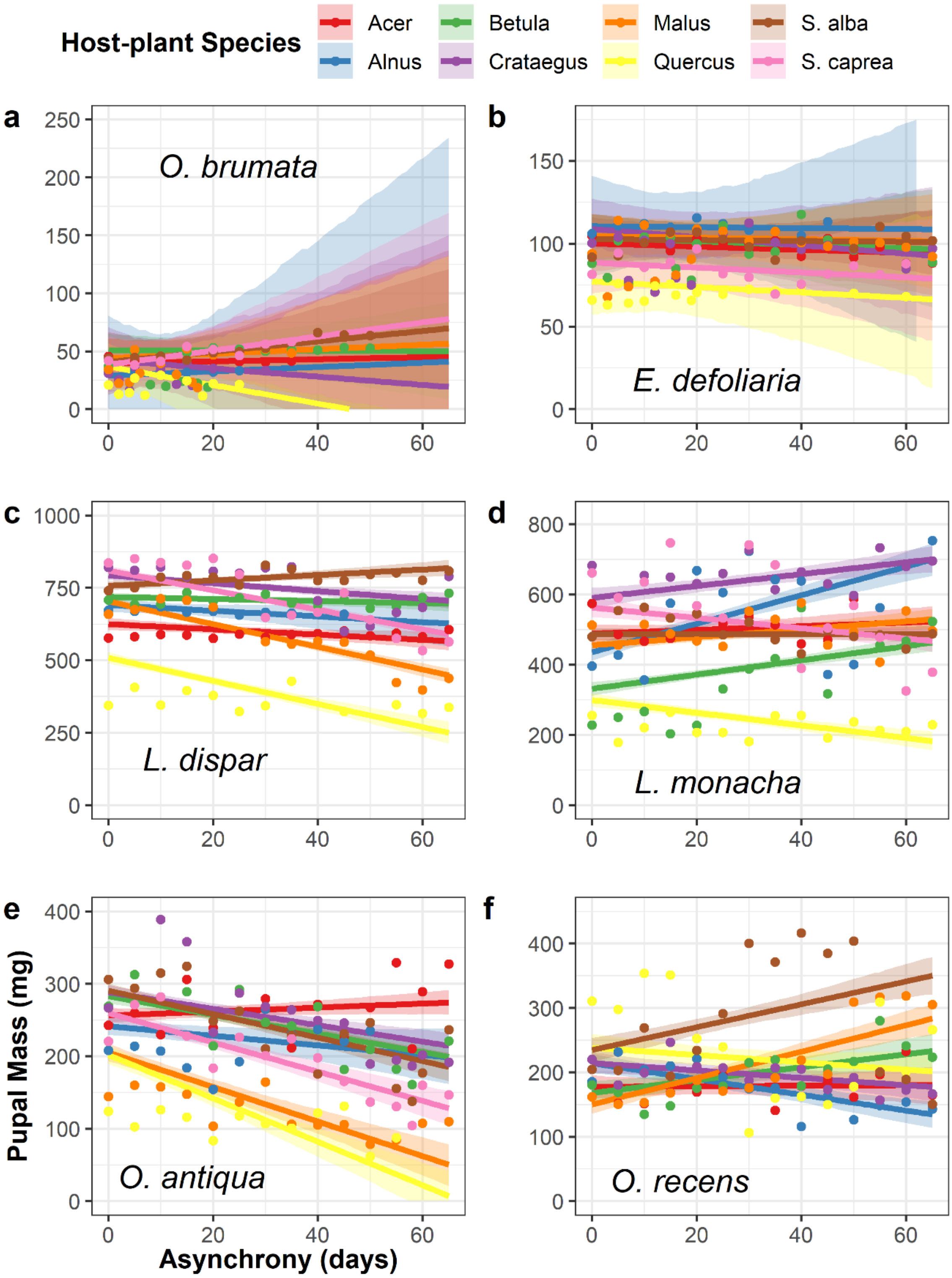


Figure 3.7. Modelled effects of asynchrony between caterpillar hatch and host bud-burst on pupal mass among caterpillar species (*a* - *f*), across eight host-plant species (± 95% CIs). Points show means of raw data. Asynchrony represents the number of calendar days after bud-burst on which the caterpillars eclosed. Estimates are shown for females only because they are most relevant for individuals of this sex.

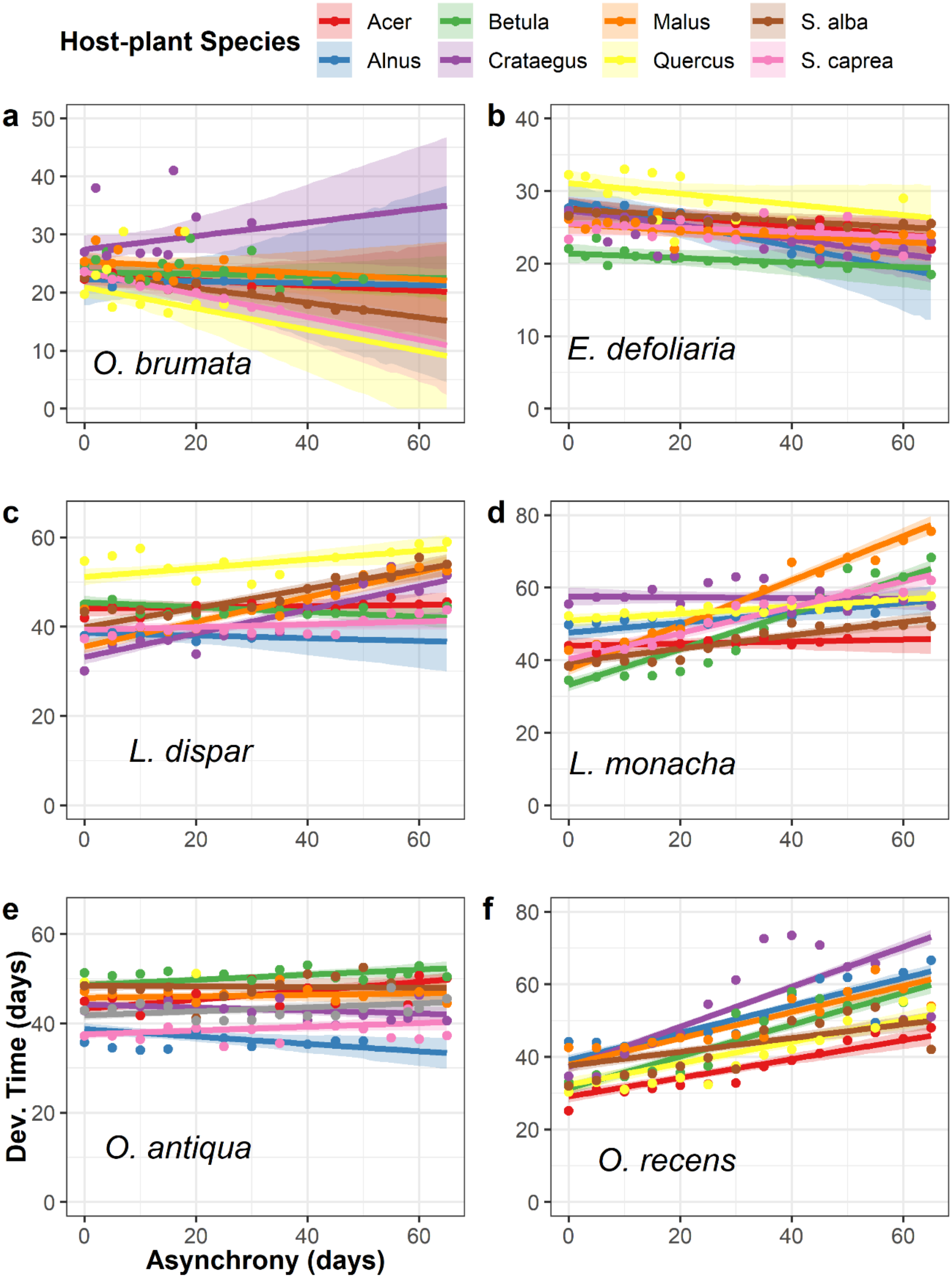


Figure 3.8. Modelled effects of asynchrony between caterpillar hatch and host bud-burst on development time among caterpillar species (*a* - *f*), across eight host-plant species (± 95% CIs). Points show means of raw data. Asynchrony represents the number of calendar days after bud-burst on which the caterpillars eclosed. Estimates are shown for females only.

suggesting that the latter is the main factor determining the negative fitness consequences of asynchrony. Particular host-plant/caterpillar combinations do often produce very idiosyncratic effects (e.g. survival of: vapourer on alder, oak and apple; mottled umber on willow; winter moth on willow and birch).

(e) Fitness in the winter moth

Using the posterior distributions of survival and pupal mass across time on each host-plant species, I estimated changes in fitness in the winter moth with increasing asynchrony (see Appendix 2). On most host-plants, fitness reached almost zero by 30-40 days (Figure 3.9). Rates of decline in fitness vary across host-plant species, with some declining precipitously from an initially high level (e.g. birch, sallow, and white willow) and others showing a more gradual, linear decline (e.g. apple and oak). On apple, fitness declines gradually over a period of two months, and still remains above zero.

3.4.2. The effects of sex on performance

Sex was only determinable for mass and for development time. Sex had no significant main effect on either the intercept (pupal mass or time taken to pupate when asynchrony = 0, or perfect synchrony) or the slope of the overall effect of asynchrony (Figure 3.2). However, estimates of sex by caterpillar species variance in the intercept and slope of the effects of asynchrony (Mass, intercept = 15100.95, CIs: 0.00, 47320.00, slope = 0.19, CIs: 0.00, 0.67; Dev. Time, intercept = 26.64, CIs: 0.00, 94.99, slope = 0.00, CIs: 0.00, 0.02) and of the sex by host-plant interaction on asynchrony (Mass, intercept = 934.13, CIs: 0.00, 2447.13, slope = 0.11, CIs: 0.00, 0.38; Dev. Time, intercept = 1.55, CIs: 0.00, 5.53, slope = 0.00, CIs: 0.00) were substantial, though the lower bound approached zero in each case. Estimates of variance in the three way interaction between sex, host, and caterpillar species were also substantial, and in many cases significant (Mass, intercept = 3891.11, CIs: 2497.10, 5467.85, slope = 1.411, CIs: 0.89, 1.97; Dev. Time, intercept = 9.12, CIs: 4.78, 14.24, slope = 0.00, CIs: 0.00, 0.00). These data suggest that in many instances the sex of an individual can act to modulate or

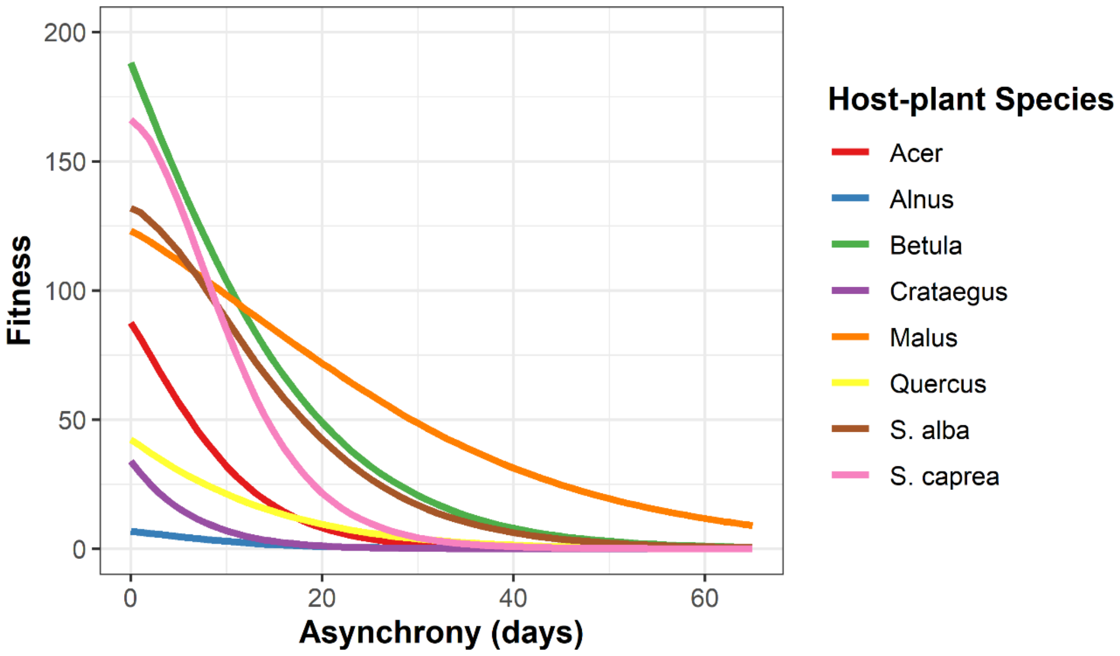


Figure 3.9. Projected changes in mean fitness with increasing asynchrony in the winter moth, across eight host-plant species. Fitness is expressed as an absolute value: an estimate of the mean number of ova produced per female assigned to a given treatment group (see Appendix 2). Asynchrony represents the number of calendar days after bud-burst on which the caterpillars eclosed. Estimates are shown for females only.

adjust the effects of asynchrony in various ways, in different caterpillar and host-plant combinations. Although it was not the main purpose of this study to explore sex-based differences in the effects of asynchrony, this highlights the need to control for this variable in analyses and the potential for the effects of mismatch to diverge between males and females.

3.5. Discussion

3.5.1. The complex effects of asynchrony on caterpillar performance

I found a strong effect of asynchrony on caterpillar survival, and lesser effects on final pupal mass or development time (Figure 3.4). The effects of asynchrony tend towards varying more among caterpillar species than among different host-plant species (Figure 3.5), implying that, whenever they hatch, the costs of asynchrony are more dependent on the caterpillar species than on the host-plant species. This suggests that generalising the effects of asynchrony across caterpillar species—such as extrapolating from the winter moth to other spring-feeding species, for example—is likely to yield misleading results. Nonetheless, caterpillars still seem able to tolerate a sizeable quantity of late hatching asynchrony—in the winter moth, which shows qualitatively the most severe declines in fitness (Figures 3.5 and 3.8), I found survival rates were still at around 25% on certain host-plants (birch and willow) for individuals hatching up to 40 days after bud-burst.

The effects of asynchrony on caterpillar fitness are still, however, in many cases, contingent on the particular host-plant and caterpillar species involved, and there can be considerable variation in performance across different host-plants within a given caterpillar species (Figures 3.5 – 3.8). This too places limits on our ability to generalise across hosts and caterpillars. To illustrate this latter point, we can see that in the vapourer moth, estimated survival probability can range from just over 10% (alder) to over 90% (birch) when hatching 40 days asynchronously, depending on host-plant species. While we can say something of the general effects of asynchrony across caterpillar and host-plant species more broadly, the interaction between these two variables also seems very important (Figure 3.5).

3.5.2. Are winter moth and oak a representative model system?

A conspicuous pattern which emerges from the results presented here is that the winter moth on oak—one of the most widely studied species-pairings in literature on the MMH (van Asch and Visser, 2007; Figure 1.2)—is more of an exceptional case than it is typical. Comparing, for example, survival across caterpillar species, we find that in the winter moth survival declines more steeply and to a greater extent than in all the other species studied here (Figure 3.6). Winter moth is among those few species that show clear overall declines in pupal mass with increasing asynchrony on oak, and reduced development time (Figure 3.7). Taken together, this perhaps suggests that asynchrony has a greater negative effect on the fitness of winter moth caterpillars than it does on other spring-feeding species—or, at the very least, those species considered in this study. In the case of oak as a host-plant, too, we see an unusual rather than a typical pattern. Survival to pupation and pupal mass are consistently among their lowest levels on this host-plant, across caterpillar species, with the exception of the scarce vapourer (Figure 3.6). It would therefore seem both unreasonable and unwise to generalise too widely from the winter moth/oak relationship to other caterpillar and host-plant species, and assume that effects observed in this one species can be extended to the entire spring-feeding caterpillar guild.

When we consider the estimated fitness of the winter moth on oak, we find that only hawthorn and alder proved less suitable hosts (Figure 3.9). Even with perfect synchrony, fitness on oak was still around a quarter of that attained on birch and sallow, for example. However, even at this very low initial level, and even though it seems that, comparatively, oak is a poor host-plant, estimated declines in fitness due to asynchrony in this experiment were not as extreme as has been suggested in other studies (see below, and Table 3.1). The view that even a slight mistiming of caterpillar eclosion, relative to the bud-burst phenology of their host-plant, has severe negative fitness consequences, and that such mistiming might increase under climate warming, has come to be a widely accepted, influential view, frequently invoked by heavily cited research (e.g. Singer and Parmesan, 2010; Chuine, 2010; Schweiger *et al*., 2010; Reed *et al.*, 2011; van Asch *et al.*, 2012; Williams *et al.*, 2012; Fox, 2013; Iler *et al*., 2013; Derks *et al.*, 2015; though for studies that suggest a lesser effect of mismatch, see Table 3.1 and: Hunter e*t al.*, 1991; Kerslake and Hartley, 1997).

Van Asch *et al.* (2007) provide the most pessimistic estimates of the fitness effects of asynchrony in the winter moth. On oak, they found that fitness declined to zero when caterpillars eclosed as little as five days asynchronously, in either direction. They found that early hatching heavily effected survival, but produced highly fecund adults; late hatching affected survival less severely, but produced smaller adults, with lower fecundity. My results do indeed indicate a slight decline in pupal mass with increasing asynchrony, but this effect occurs over period of weeks. In contrast to van Asch *et al*., I also find a clear effect of late-hatching asynchrony on survival. Overall I estimate that fitness declines at a much more gradual rate, tapering off, and that it does not reach zero in this experiment until caterpillars hatch approximately thirty calendar days after bud-burst. This paints a very distinct picture to van Asch *et al*.'s symmetrical fitness profile, where it is the combination of high survival *and* high pupal mass at perfect synchrony that produces the fitness optimum, and thus selection for synchronous timing. Tikkanen and Julkunen-Tiitto (2003) also estimated the fitness of winter moth caterpillars hatching at various degrees of asynchrony in a lab experiment. As in my experiment, but in contrast to van Asch, they find declines in both mortality and predicted realised adult fecundity. Tikkanen and Julkunen-Tiitto (2003) compute a superficially similar fitness profile to van Asch et al. (2007), but express the extent of asynchrony in degree days. Fitness declines precipitously, and reaches zero by 100dd (this equates to twenty days at ambient temperatures of 10°C, or ten days at 15°C, with a 5°C baseline). This is a steeper decline than I have estimated from my results, but less steep than that estimated by van Asch *et al.* (2007).

It is not entirely clear why the results from both of these studies (Tikkanen and Julkunen-Tiitto, 2003; van Asch *et al.*, 2007) and those presented here differ so substantially. Some key differences in the experimental approaches taken include: (i) differences in rearing temperature (ambient at Banchory, UK [Tikkanen and Julkunen-Tiitto, 2003], at or below 20°C [van Asch *et al.*, 2007], and 17-21°C [here]), which could induce different responses due to stress, such as higher levels of mortality; (ii) geographical variation in performance responses between the different populations, which I have previously shown to be important in Chapter 2; and, (iii) a small sample size of trees from which foliage was collected, which may differ between treatment groups (~10 [Tikkanen and Julkunen-Tiitto, 2003], 3 or 6 [van Asch et al., 2007], and ~15 [here]). The secondary chemistry of foliage from individual trees, even of the same species, can differ due to environmental factors including microclimate, soil chemistry and moisture levels, and leaf growing conditions such as sun or shade (Henriksson *et al.*, 2003; Tikkanen and Julkunen-Tiitto, 2003; Laitinen *et al.*, 2005; Peltonen *et al.*, 2010; Gaytán *et al.*, 2022). Such differences can result in significant within-tree variation in the performance of the caterpillars feeding on them (e.g. Suomela *et al.*, 1995). The effects of phenological stage on caterpillar performance can potentially be confounded by the genetic and environmental idiosyncrasies of each individual tree. Indeed, Tikkanen and Julkunen-Tiitto (2003) show a considerable quantity of variation in mortality and predicted fecundity produced by different individual trees at the same phenological stage—thirty degree days after bud-burst, caterpillar survival ranged from 0 to 60%, depending on which tree they were reared from.

3.5.3. Buffering against mismatch and climatic change

This study is the largest experimental investigation of the effects of trophic mismatch in spring-feeding caterpillars yet conducted, in terms of the numbers of individual caterpillars used and the range of caterpillar and host-plant taxa involved—this gives us a unique opportunity to draw some meaningful conclusions about the importance and ubiquity of trophic mismatch. Synchrony between the timing of caterpillar hatch in spring and the appearance of foliage on their host-plant is clearly important for the fitness of these spring-feeding species (Figure 3.2). The degree of synchrony can, in turn, potentially influence or drive fluctuations in their abundance in the field (Varley *et al.*, 1974; Wesołowski and Rowiński, 2008; Kulfan *et al.*, 2018). On the whole, however, my results suggest that many caterpillar species show at least some degree of tolerance and resilience in the face of mismatch, in contrast to the view often posited in the literature. The precise fitness effects of asynchrony, in fact, depend on a complex set of interacting variables, including host-plant species (see Chapter 2), host-plant individual (see Chapter 5), caterpillar species (Figures 3.4 – 3.6), geographical locality (see Chapter 2), and local environmental conditions.

Buffering against mismatch at an individual and population level means that, for these caterpillars, the shape of the fitness landscape across the spring and early summer months, rather than a narrow “peak”, seems, more precisely, to resemble a kind of *plateau*—temporally ephemeral, but broader and flatter, perhaps asymmetrical, and tapering off more gradually at either side. Because of their polyphagous diet, individual caterpillars can deal with finding themselves on a wide range of host-plant species, and can tolerate, to a certain extent, maturing foliage (though this ability also depends on the plant species). At a community level, surveying across the caterpillar guild, polyphagy, resilience to mismatch, and species-specific differences in these attributes, means that caterpillar populations as whole will be more stable throughout spring in the face of environmental unpredictability, with implications for species at higher trophic levels.

Timing matters, then, but within fairly broad bounds. Even the winter moth seems to be surprisingly resilient to mistiming, though it is comparatively one of the least resilient species in this study (e.g. Figure 3.6). Indeed, this kind of resilience may be a necessary trait for species occupying such an uncertain and variable niche, allowing them to exploit a narrow phenological window. An inherent robustness in the face of various degrees of asynchrony could equally well act to buffer individuals and populations against any increased occurrence of mistiming in future, as a result of climate change and varying phenological sensitivities to temperature.

3.5.4. Asynchrony in other spring-feeding caterpillar species

Most previous work on the effects of asynchrony in spring-feeding caterpillars has focused on pairwise relationships over a limited range of species, particularly those of economic importance. Of the species I have studied here other than the winter moth, only the effects of asynchrony in the gypsy moth has received attention previously. I found clear declines in gypsy moth caterpillar survival across several months of asynchrony on most host-plants, though declines in pupal mass in only a couple of species (oak and apple; Figures 3.6 and 3.7). Development time largely remained stable with increasing asynchrony, but increased clearly on a handful of hosts (willow, apple, hawthorn and perhaps oak; Figure 3.8). As in the winter moth, oak appears to be among the poorest host-plant species. In contrast, Barbosa and Capinera (2011) found that caterpillars fed on red oak *Quercus rubra* produced pupae almost twice as large as those on red maple *Acer rubrum*. Other work suggests that red and white oak *Quercus alba* can be sub-optimal host-plants when compared with birch *Betula populifolia* (Barbosa and Greenblatt, 1979). Here, I found that pupal mass is lower on *Q. robur* than on either *B. pendula* or *A. pseudoplatanus*.

Raupp *et al.* (1988) found that survivorship and pupal mass across three host-plants (white oak, hickory *Carya tomentosa,* and red maple) declined with increasing asynchrony, but over a period of several weeks. American beech *Fagus grandifolia*, a moderately good host-plant, remained suitable for caterpillars to establish themselves on only for a period of one week, after which rates of survival dropped to zero—a steeper decline than I found on any host-plant (Figure 3.6). The duration of larval development increased with increasing leaf age but, counter-intuitively, so did pupal mass (Raupp *et al.*, 1988). Hunter and Elkinton (2000) looked at North American populations of the gypsy moth on black *Quercus velutina* and white oak, and found that when reared in captivity, survival only declined with a high degree of late hatching asynchrony. In a similar compensatory mechanism to that which has been suggested for the winter moth (Tikkanen and Julkunen-Tiitto, 2003; van Asch *et al.*, 2007), caterpillars hatching too early suffered high levels of mortality, but had increased fecundity as adults (since those which did survive were able to exploit young, nutritious foliage), while late hatching adults had low mortality but low fecundity (Hunter and Elkinton, 2000) (cf. Figures 3.6 and 3.7). This produces a fitness profile optimised on hatch/bud-burst synchrony, but the effects operated over an extended calendar period, with eventual fecundity declining by

~25% over the course of a month. However, when exposed to field conditions, this apparently strong selective pressure for synchrony was disrupted by high levels of density-dependent mortality due to parasitism, decreasing survival where baseline mortality due to host-plant palatability was low (Hunter and Elkinton, 2000). The ultimate fitness effects of asynchrony, therefore, were largely mediated by the action of natural enemies and not the host-plants themselves in this instance. It is possible that a similar mechanism could operate more widely in other species, levelling out or ameliorating any apparently strong selection for synchrony we find in the lab—this may go some way to explaining discrepancies between experimental fitness assays and field studies of abundance.

Not all studies of mismatch find even qualitatively similar results, however. Gypsy moth caterpillars have been found, for example, to have higher growth and survival rates, by a considerable margin, on *older* foliage when fed on cottonwood *Populus angustifolia* (Meyer and Montgomery, 1987)—indeed, this is not a solitary observation and has been made in other species (e.g. the western tent caterpillar; Sarfraz *et al.*, 2013). In other moth species, fitness has been shown to improve when caterpillars are reared on foliage of a range of different phenological stages (e.g. the North American whitemarked tussock moth *Orgyia leucostigma* on balsam fir *Abies balsamea*; Johns *et al.*, 2009). Such findings run contrary to the idea that synchrony is universally important and emphasise the contingency of the effects of asynchrony on ecological and environmental factors.

Synchrony assays have been conducted on only a handful of other spring-feeding caterpillar species, typically periodically out-breaking taxa, such as the western spruce budworm *C. occidentalis,* the eastern spruce budworm *C. fumiferana*, the forest tent caterpillar *Malacosoma disstria*, and the eastern tent caterpillar *M. americanum*. In this literature generally, we find the same pervasive trend which is very much in agreement with the findings I have presented here: for spring-feeding caterpillars, timing is important, and late hatching does typically result in negative consequences for some aspect or aspects of caterpillar performance—higher mortality, lower pupal mass (and, hence, in females, fecundity), and an extended period of larval development. However, in spite of a few exceptions (Schneider, 1980a; Quiring, 1992; Fuentealba *et al.*, 2018), these effects are usually not severe until the degree of asynchrony reached is very substantial, on a scale of weeks, and perhaps months, rather than days (Blake and Wagner, 1986; Schroeder, 1986; Foil *et al.*, 1991; Parry *et al.*, 1998; Haukioja *et al.*, 2002; Chen *et al.*, 2003; Klemola *et al.*, 2003; Sarfraz *et al.*, 2013; Kharouba *et al.*, 2015; Régnière and Nealis, 2018). On coniferous trees too, where spring growth occurs differently, performance is typically optimal on the current year's growth, relative to more mature foliage (Dodds *et al.*, 1996; Pinault *et al.*, 2009; though cf. Johns *et al.*, 2009).

3.5.5. The interpretation of development time

Of the three fitness metrics measured in this experiment, the impact of changes in development time on overall fitness is perhaps the least easily established—while it almost certainly does have an effect, changes can be ambiguous in their consequences. Development time in caterpillars may either shorten (Goulson and Cory, 1995; York and Oberhauser, 2002) or extend (Kukal and Dawson, 1989; Moreau *et al.,* 2006; Bawin *et al.*, 2016; reviewed in Awmack and Leather, 2002) under sub-optimal conditions: individuals may speed up their progress to pupation, and pupate at a smaller size, in order to escape stressful conditions, such as a nutritionally poor host-plant; on the other hand, feeding on a nutritionally poor host-plant might cause a protracted developmental period where a minimum threshold of size must be reached before pupation. This potentially divergent response in different species (and perhaps under different biotic and abiotic environmental conditions) might account for some of the variation we see modelled in this metric—the between-host-plant trends in development time with asynchrony are qualitatively similar in their direction, but between caterpillar species this trend can vary in direction, perhaps indicating that these different responses operate in different species (Figures 3.3 and 3.4). I estimated fitness in the winter moth using survival and pupal mass only (see Appendix 2) because it is difficult to see how to properly include development time in such a calculation without some *a priori* understanding of the extent to which developing caterpillars are *more* exposed than pupae to mortality (predation, parasitism, disease), for example, or their particular developmental response under stressful conditions.

3.5.6. Implications for trophic mismatch in other systems

The idea that climate warming may increase the occurrence of trophic mismatch in natural systems, resulting in population declines, is frequently suggested in the literature, but currently the evidence to properly support this hypothesis is lacking (Samplonius *et al.*, 2020). In the case of the woodland tri-trophic food chain, the evidence presented here suggests that one key criteria for the MMH to operate—that a consumer relies on an ephemeral resource (Cushing, 1969, 1990; Samplonius *et al.*, 2020)—only partially stands up to scrutiny. Caterpillars exploit a range of phenologically variable host-plant species and can tolerate sometimes substantial degrees of asynchrony; for their bird predators, the caterpillar fauna is composed of a range of different species, with different phenological responses to climate change, and, being buffered against mismatch, show some persistence in the face of environmental change. Even in this classic phenologically synchronised system many of the species show clear evidence of robustness to mistiming: the extent to which buffering exists in other communities and ecosystems has yet to be properly appreciated. Given the general lack of evidence to support the idea that climate change may harm populations by increasing mismatch (Samplonius *et al.*, 2020), it seems prudent that we do not assume this will be the case *prima facie*, even in apparently phenologically synchronised systems. Further, the differences we see among host-plant and caterpillar species in the effects of asynchrony—particularly how atypical the standard winter moth/oak relationship may be—highlights the importance of understanding more broadly the ecology of a given system, and not just a single aspect of it, before attempting to forecast the effects of future environmental changes. These results challenge us to re-evaluate our preconceived ideas about the effects of climate change on ecosystems, and particularly the role of mismatch under increasing temperatures.

Chapter 4: Strategies to buffer the impacts of early hatching—starvation tolerance and the exploitation of host-plant buds

4.1. Abstract

The foliage of many tree species is at its most vulnerable in early spring because it does not yet possess the anti-herbivory defences that develop later in the season. This offers a rich but temporally ephemeral resource for phytophagous species able to exploit it. But timing when this new foliage will appear can be difficult, and the fitness consequences of asynchrony can be severe. Spring-feeding caterpillars are an important, keystone guild in temperate woodlands and at the centre of many food webs. Faced with early-hatching asynchrony, caterpillars can either tolerate starvation until foliage appears, disperse to a new location in hopes of finding palatable foliage, or bore into or otherwise exploit the unopened buds of their host-plants. Here, I experimentally tested two of these mechanisms: first, I determined the starvation tolerance of five British spring-feeding caterpillar species and considered how these limits are affected by temperature; second, I experimentally tested the ability of winter moth *Operophtera brumata* caterpillars to exploit unopened or partially open buds of a range of host-plant species as a food source. I found that starvation tolerance varied considerably across the species assayed, from several days to several weeks. Spring-feeding caterpillars show a continuum of starvation tolerance, from those extremely robust to those extremely sensitive in the face of starvation. Significantly, starvation tolerance is lowest in the winter moth, which is frequently taken as a representative model species for the entire guild. Although buds become increasingly useable as they develop and expand, caterpillars can still begin feeding on closed buds, albeit to a much lesser extent. These two mechanisms may help buffer caterpillars against the unpredictability of environmental conditions in spring and the negative fitness effects of mismatch with their host-plants. Crucially, they may also provide these species and their populations with some degree of resilience in the face of any increased incidence of mismatch in future as a result of climate warming.

4.2. Introduction

The onset of the growing season in temperate climates marks a dramatic shift in resource availability for species dependent on plants, such as phytophagous insects. Insects can only make use of this newly abundant, but temporally ephemeral, resource if they are able to time their appearance to match. At its most general, this is reflected in the fact that most phytophagous insects occur during the summer months, when abiotic conditions (e.g. temperature) are favourable and plant resources are abundant. Insects are highly significant antagonists in the life of almost all plant species, causing disease, tissue damage, and sometimes complete defoliation (Schoonhoven *et al.*, 1998). The arms race in which these two groups of organisms have been engaged has run since arthropods first made the move onto land over four hundred million years ago. Terrestrial plants have developed an array of chemical and structural adaptations to avoid or deter herbivory (e.g. Juniper and Southwood, 1986). Within the broad time window during which plant foliage is available for consumption, then, there is distinct temporal variation in its composition, abundance and palatability, such that selection can act on insects to promote phenological synchronisation at a much finer time scale.

In spring, buds burst on deciduous trees, and the young, developing leaves open and expand to their full size. Throughout this process, and afterwards, leaves undergo biochemical and structural changes. They accumulate defensive secondary chemicals such as tannins, and the relative proportions of key metabolites, such as water, nitrogen, and various proteins, vary considerably, affecting the nutritional value of their tissue for herbivores (Feeny, 1968; Kerslake *et al.*, 1998; Ruuhola *et al.*, 2001; Tikkanen and Julkunen-Tiitto, 2003; Strengbom *et al.*, 2005). Structurally, leaves toughen which makes them less digestible and means that it is more difficult, particularly for smaller, neonate caterpillars to consume them (Feeny, 1970). This process of maturation (with the accompanying biochemical and structural changes) occurs gradually at the onset of the growing season, and the speed and extent to which it occurs varies between plant species, individuals, and under different environmental conditions (e.g. Kramer, 1995; Karlsen *et al.*, 2007; Vitasse *et al.*, 2009; Polgar and Primack, 2011; Basler and Körner, 2012; Cole *et al.*, 2015; Cole and Sheldon, 2017; Denéchère *et al.*, 2018; Geng *et al.*, 2020). Leaf maturation has the effect of making leaves overall less palatable such that, for species adapted to the early flush of less defended leaves (which are less suited to coping with late-season plant defences, e.g. see Schroeder, 1986) there is a much narrower time window during which leaves are of acceptable palatability. The consequences of mistiming can be severe—caterpillars which hatch too early in spring fail to find food and can starve, while those hatching too late are forced to feed on maturing foliage of reduced palatability, and suffer reduced fitness (Thomson, 1954; Embree, 1965; Feeny, 1970; Varley *et al.*, 1974; Tikkanen and Julkunen-Tiitto, 2003; van Asch and Visser, 2007; van Asch *et al.*, 2007).

In spring-feeding caterpillars, an ecologically and economically significant guild of herbivores, the timing of egg hatching is predominantly driven by temperature (van Asch and Visser, 2007). In the winter moth *Operophtera brumata*—a widespread, abundant, Palearctic geometrid moth, which is a commonly used model species—hatching phenology is entirely dependent on temperature (Kimberling and Miller, 1988; van Asch and Visser, 2007; van Asch *et al.*, 2012; Hibbard and Elkinton, 2015; Salis *et al.*, 2016). Fitzgerald (1995) proposed that changes in plant volatiles might allow eggs to time their hatching based on direct cues from host-plant development (e.g. bud-burst on proximate buds), but there is no evidence for this (Abarca and Lill, 2015) or that caterpillars can use any other direct, proximate cues to trigger hatching (Buse and Good, 1996). Mirroring the temperature cues used by their hosts for development, therefore, seems to be the principal means by which caterpillars synchronise their timing. However, if climate warming affects the phenology of caterpillars and their host-plants differently (van Asch *et al.*, 2007, 2012), then phenological asynchrony could result, with potentially negative fitness consequences for the caterpillars. If this translates into negative population-level consequences, the deleterious effects of asynchrony could ripple up the food chain to the higher trophic levels which depend on caterpillars, in turn, as a food source (Durant *et al.*, 2007). The negative effects of asynchrony that might be induced by temperature change, however, may be ameliorated if caterpillars can tolerate asynchrony of varying degrees. In Chapter 3, I considered in detail the effects of late hatching, relative to host bud-burst; how this affects performance on individual hosts; and what the population-level consequences might be. Compared with the effects of late hatching, the unique problems posed by early hatching have received comparatively little attention in the literature. Indeed, It could potentially impose a harder selective boundary than late hatching (Singer and Parmesan, 2010), if it is more difficult for neonate caterpillars to endure a complete absence of food, than simply food of gradually declining quality. For example, Tikkanen and Julkunen-Tiitto (2003) found fitness declining more rapidly with early hatching than late hatching, generating an asymmetrical fitness profile (though cf. van Asch *et al.*, 2007, who estimated a symmetrical fitness profile).

The simplest mechanism newly hatched spring caterpillars could employ to deal with early hatching asynchrony is to endure a period without food, waiting until foliage becomes available that they can then exploit (Young, 1997). The green oak tortrix moth *Tortrix viridana*, for example, has been found to survive for up to 10 days without food, under typical spring time conditions (Hunter, 1990), which matches typical within-year variation in the bud-burst dates of its host-plant, English oak *Quercus robur* (Ivashov *et al.*, 2002). Asynchronous hatching, therefore, may not exert considerable fitness effects on populations of this species, unless the degree of mistiming exceeds 10 days. Environmental conditions, such as temperature and humidity, can significantly affect the duration of any period of starvation tolerance (e.g. Patocka, 1972; Wint, 1983; Hunter, 1990). Low temperatures generally reduce developmental and metabolic rates in Lepidoptera (Majerus, 2002) and, particularly for smaller larvae, high temperatures can lead to desiccation or physiological stress (Woods and Singer, 2015). Typically, increased humidity increases starvation tolerance, though species inhabiting dry environments can often tolerate exceptionally low relative humidity (Woods and Singer, 2015). Degrees of starvation tolerance under identical environmental conditions can vary considerably among species—Reavey (1992), in a study of 42 species of British Lepidoptera, found that neonate caterpillars could survive from as little as 1 day up to 20 days without food, depending on species. If climate change results in phenological asynchrony between spring-feeding caterpillars and their host-plants, the ability to survive for weeks without food could provide a buffer against the worst fitness effects.

A second mechanism by which early hatching caterpillars may cope is by utilising the unopened or partially opened buds of their host-plant as a food source. Generally, literature dealing with phenology and phenological synchrony conceptualises ‘bud-burst’ or ‘bud-break’ as a clear, discrete event—but the transition from tough, completely closed, overwintering bud to a small cluster of unfurling leaves is gradual. Buds are produced by plants—particularly woody plants in temperate climates—to enclose embryonic shoots, leaves, or flowers, throughout a dormant period (Lowson, 1946; Mauseth, 1988). These buds are usually covered by bud scales or cataphylls, specialised structures that enclose the delicate tissues of the bud, protecting them from damage due to winter temperatures, insects, or desiccation from high winds (Mauseth, 1988). The epidermis or cuticles of the bud scales are thickened, or they are covered in a layer of corky bark—the latter increases water retention and is inedible by insects (Mauseth, 1988). For these purposes, bud scales can also exude oils and resins (Curtis and Lersten, 1974). However, bud structure, morphology, and rate of phenological development (Lechowicz, 1984; Kramer, 1995; Panchen *et al.*, 2014; Roberts *et al.*, 2015; Cole and Sheldon, 2017) can differ considerably across species. Indeed, buds can lack scales entirely, exposing the tissue underneath—so-called *naked buds*—a phenomenon more widespread in temperate environments than previously thought (Schoonderwoerd and Friedman, 2021). At the plant population level, therefore, there is a great deal of variation in the onset of 'bud-burst', and consequently in the availability of foliage for caterpillars (e.g. Karlsen et al., 2007; Cole et al., 2015). Variation in bud morphology across different plant species also likely affects their vulnerability to attack and exploitation by insects.

There is an interesting contrast in the literature dealing primarily with entomology on the one hand, and phenology on the other, in the extent to which plant buds are thought of as suitable sources of food for spring-feeding caterpillars (Table 4.1). In the case of the winter moth in particular, studies examining phenological asynchrony and the MMH emphasise the inability of neonate larvae to feed unless buds are open; entomological literature, giving accounts of the biology and ecology of the caterpillars, repeatedly asserts that neonate larvae hatching too early can "bore into" or otherwise consume the unopened buds of their host trees (Table 4.1). Indeed, bud-boring behaviour is widespread among the caterpillars of the smaller moth species (Maitland Emmet and Heath, 1992; Langmaid *et al.*, 2018). These two claims are apparently mutually exclusive, and have very different implications with regards to the sensitivity of the winter moth and other spring-feeding species to early hatching asynchrony. I can find no explicit attempt in the literature to experimentally test the ability of neonate caterpillars to exploit tree buds at various stages of development, although observational and anecdotal evidence has been reported.

Here, using captive rearing experiments, I examine these two mechanisms by which early hatching caterpillars may be able to cope with the sub-optimal conditions they find themselves in. First, I test the effects of temperature on the ability of neonate caterpillars

Table 4.1. Contrasting perspectives in the entomological and phenological literature on the ability of winter moth larvae to exploit unopened buds on deciduous trees. Many of these studies simply assert that caterpillars hatching too early cannot exploit unopened buds, without providing evidence. Those which do, frequently cite Feeny's (1970) work, as is evident below. He himself, however, simply asserts the high mortality associated with hatching too early, and makes no attempt to test the hypothesis. Comments in square brackets are my own.

Divergent views on the consequences of early hatching
Entomological Literature
"The caterpillars are extremely small at first, and suspend themselves by threads. They commence their destructive career by eating into the young, unexpanded buds." **Stokoe (1948b)** "First-instar larvae feed on the opening buds but drift with the wind else-where on silken threads if the buds are closed. Newly hatched larvae can live for five days with no food." **Cuming (1961)** "[T]he highest [mortality] in the Winter moth in Wytham Wood is usually winter disappearance due to the starvation that results when Winter moth eggs hatch before the buds of their food trees have burst" **Majerus (2002)** "The larvae hatch during April and bore into the developing buds, feeding within until the food supply is exhausted and then moving to another bud or on to the young leaves" **Porter (2010)**
Phenological Literature
"Numbers of hatching larvae which survive on the foliage are controlled by the degree of synchronism between insect and host phenology; larvae that hatch early starve because they cannot feed on the closed buds." **Embree (1965)** "If the majority of the trees open their buds later than the peak egg hatch, a high mortality of caterpillars results, since the young larvae are unable to penetrate the closed buds." "The average annual mortality of winter moth due to this winter disappearance is about 90% (G. R. Gradwell, *personal communication*), largely made up of larvae hatching too soon to enter the oak buds. This high mortality of first instar larvae, together with subsequent competition for food, seems a high biological "penalty" to pay to ensure that the remaining larvae commence feeding on the leaves at the earliest possible chance, and presumably it must be offset by some considerable selective advantage for early feeding". **Feeny (1970)** *cont.*

"When oak buds are beginning to open in early April the eggs hatch and we find the first stage caterpillars feeding in the buds, where they do great damage to the tiny leaves"
Varley *et al.* (1974)

"The highest mortality of the winter moth, during this annual life cycle, occurs as a result of failure of freshly-hatched larvae to find suitable food. The first instar larvae are unable to penetrate oak buds which have not yet begun to open, nor are they likely to survive on young leaves which are already a few days old and have begun to toughen."
Feeny (1976)
[The latter point, about the extreme unsuitability of even slightly matured leaves, seems to be an outlying and very extreme view]

"Should the larvae hatch either before or after the oak leaf flush, they will be unable to find sufficient young leaves and so their survival will depend on the ability of the first instar caterpillars to locate and become established on alternative host-plants."
Wint (1983)

"On the other hand, if the eggs hatch before bud burst, the first instar larvae must become established on alternative host plants in order to avoid starvation."
Kirsten and Topp (1991)

"It is obvious that, in such situations, the caterpillars will starve if the eggs hatch before budburst. Two other factors also limit the period over which oak is a suitable food: the first-instar larvae are minute (head-capsule width 0.25 mm) and so are only able to feed on very young leaves; and they must complete feeding before condensed tannins increase in the leaves (Feeny, 1968) and before leaf toughness increases (Feeny, 1970)."
Buse and Good (1996)

"If hatching occurs before budburst, larvae cannot enter a bud and have to disperse, probably resulting in high mortality"
Dongen *et al.* (1997)

"If the eggs hatch prior to bud burst the caterpillars will starve, whereas if hatching occurs after bud burst the caterpillars will have to eat less digestible leaves due to increased tannin concentrations (Feeny, 1970)"
Visser and Holleman (2001)

"If larvae emerge too late after bud burst, their future growth will be much lower […] However, the eggs must also not hatch too early, because neonate larvae do not tolerate starvation for long periods (2–5 days according to Hunter, 1990)."
Tikkanen and Julkunen-Tiitto (2003)

"If the eggs hatch before the buds are open, there is no food for the caterpillars, and they will starve to death."
van Asch and Visser (2007)

"Even a few days' difference between egg hatching and oak (*Q. robur*) bud opening has marked fitness consequences"
van Asch *et al.* (2012)

Table 4.1 cont.

from five different spring-feeding species to tolerate starvation. Second, using winter moth caterpillars in lab cultures, I test the ability of neonate larvae to feed on the buds of nine different host-plant species, at a range of phenological stages. Prior to this experiment, I developed a functional, categorical classification of bud phenology based on the gradual exposure of leaf tissues to attack by insects (see Table 4.2). Finally, I consider how these strategies might serve to buffer spring-feeding caterpillars against the negative effects of asynchrony in nature, which may become more frequent in future as a result of climate change.

4.3. Methods

4.3.1. Source and treatment of livestock

In the starvation experiment (Experiment 1), I used livestock from five phytophagous, externally feeding British moth species, from two families: the winter moth *Operophtera brumata*, the mottled umber *Erannis defoliaria* (both Geometridae); the gypsy moth *Lymantria dispar*, the black arches *Lymantria monacha*, and the scarce vapourer *Orgyia recens* (all Erebidae) (Appendix 7). These species are generally widespread and common in Britain and all have larvae which feed in early spring. All overwinter as ova except the scarce vapourer, which passes this period as a diapausing first instar larva (Skinner, 2009; Porter, 2010; Waring *et al.*, 2017; Henwood *et al.*, 2020). In the experiment to test the ability of neonate larvae to utilise buds (Experiment 2) I used caterpillars of the winter moth only, a frequently used model species in the literature (van Asch and Visser, 2007).

I collected female winter moths between 25 Nov 2019 and 8 Jan 2020 in the Hermitage of Braid LNR (Edinburgh) using lobster-pot style trunk traps, modelled on those described by Varley *et al.* (1974), which intercepted females as they ascended trees after eclosion (see Appendix 9). After collection females were placed individually in 75 x 25mm glass phials with a wad of cotton at the bottom to act as an egg laying medium. Previous trials suggested this resulted in individuals laying the maximum number of eggs relative to a range of other commonly used media. Females were stored at ~5°C in a refrigerator in complete darkness and allowed to lay freely. Approximately one month later, all tubes were examined and the dead females were removed. Ova from a total of 126 females from the Edinburgh site were obtained. Ova (or larvae, for the scarce vapourer) were obtained for the remaining species from entomologists or entomological supply companies across the United Kingdom. For each species, individuals were obtained from at least ten distinct, outbred broods. Most were sourced solely from a single population, though the source population differed between species (see Appendix 1, Table S3.3. Livestock from the year 2019/20).

Ova/larvae of all species were stored at ~5°C as and when gathered to prevent early hatch or diapause break. As required for the experiment, ova were removed from cold storage and placed at room temperature (ranged from 17-21°C) to stimulate egg hatching. A subset of ova, sampled from across all broods, were removed concurrently and allowed to hatch. Being exposed to relatively high temperatures helped ensure individuals hatched at the same time, despite inter- and intra-brood variation in the temperature requirements for eclosion (for example, in winter moth see Tikkanen and Julkunen-Tiitto, 2003). Larvae were assigned at random to each treatment group, and subsequently to each rearing culture within that treatment group.

4.3.2. Experiment 1: the effects of temperature on starvation tolerance

Neonate caterpillars were segregated within 24hrs of eclosion into 75 x 25mm glass phials, in groups of five individuals (a “culture”). Twenty caterpillars from each of the five caterpillar species were housed at two temperature treatments, 5°C and 21°C. Mean maximum and mean minimum temperatures recorded at Edinburgh, UK, from 1922-2014 were 5-12°C in April and ~7-15°C in May (*Regional Climate Summaries: Eastern Scotland*, n.d.).

The 5°C treatment was achieved using a Russell Hobbs RHCLRF17 tabletop refrigerator. To achieve the 21°C treatment, I placed phials in an insulated polystyrene box indoors, adjacent to the refrigerator. Temperatures were periodically recorded in both cases and ranged from 4-7°C and 19-21°C respectively.

Most phials were checked and caterpillar survival recorded at two day intervals, but those containing winter moth and mottled umber caterpillars at 21°C were checked daily (pilot experiments suggested survival in this treatment group would be of a very short duration). Caterpillar survival was determined by gently prodding each individual with a fine paint brush. Individuals which displayed clear, unambiguous movement in response (e.g. crawling away) were recorded as living. Individuals which showed no response were assumed to be dead or dying.

4.3.3. Experiment 2: the ability of neonate winter moth caterpillars to exploit developing host buds

Bud-burst is a difficult phenomenon to precisely define and delimit. Typically, studies classify stages of bud development on a qualitative, categorical scale (e.g. Embree, 1965, in the N. American red oak *Q. rubra*). Difficulties arise, however, when we try to define analogous stages across different plant species, when these can differ significantly in morphology, internal structure, and the ways in which they develop. Previous attempts at creating standardised ‘phenophases’ have therefore used a much coarser scale, e.g. “breaking leaf buds” and “young leaves” (Denny *et al.*, 2014). Here, I tested the ability of neonate winter moth caterpillars to become established on buds of different developmental stages across nine known host-plant species, which are common and widespread in Britain: alder *Alnus glutinosa*, apple *Malus domestica*, birch *Betula pendula*, cherry *Prunus avium*, hawthorn *Crataegus monogyna*, oak *Quercus robur*, sallow *Salix capraea*, sycamore *Acer pseudoplatanus*, and willow *Salix alba* (Appendix 7). I developed a functional system based on morphological steps which may be passed through in bud development which are fairly easy to identify and which mark steps in the gradual increase in the amounts of green tissue exposed (Table 4.2. and Figure 4.1). This green tissue is that most likely to be attacked by caterpillars.

Buds were collected as cuttings in the field in April, and immediately placed in sealed plastic bags. The cut end of each bud was wrapped in moist tissue and sealed under cling film. Buds were collected in the field over a period of four days and the experimental treatments were conducted concurrently (Appendix 1, Table S4.1.). At least five buds of each species were added to small 75 x 50 x 15mm transparent plastic rectangular containers. Twenty winter moth caterpillars were assigned to buds of each developmental stage on each host-plant, divided into cultures of five individuals. Bud cuttings were replaced with freshly collected buds at two day intervals. After 5 days, the number of larvae *established* on the buds was recorded—establishment was interpreted as caterpillars having survived the five day period,

Table 4.2. A functional classification of tree bud development, viewed as a food source for phytophagous caterpillars. Defining a single point of bud-burst is operationally difficult, due to inter- and intra-specific variation in morphology and development. Bud-burst describes a point on a continuum of leaf development, from fully dormant bud to fully expanded leaf. The ability of caterpillars to exploit developing buds as a food-source may vary quantitatively across these stages, in contrast to a simple MMH model whereby they can feed on buds which are "open" and cannot feed on those which are "closed". The system I develop here is based on a much finer scale than those, for example, using 'phenophases', that define only broad stages such as bud-burst and the appearance of recognisable young leaves (Denny *et al.*, 2014).

Bud Development Stage	Description	Functional Significance
0	Bud completely closed, in overwinter stage	Buds in long-term overwinter state, likely to be most resistance to extreme environmental conditions (e.g. frost) and insect attack
1	Bud swelling and expanding; newer scales, often photosynthetic, can protrude from expanding bud	Tougher scales often given way to softer, more vulnerable tissues which, as buds swell, are newly exposed; photosynthetic (less woody) tissue may be more vulnerable to attack
2	Bud continues to swell; scales begin to part and foliage tips just visible within	Cracks in the solid structure of the bud could allow the smallest insects to enter and feed on the developing leaf tissue within, while also providing shelter from predation
3	Bud opens wider; foliage clearly visible protruding	As above; foliage becoming more easily accessible; internal bud feeding will provide progressively less shelter
4	Bud fully open; foliage protruding and spreading; small leaves clearly taking on true shape	Foliage fully available to insect attack; far less shelter offered by bud and developing leaves.

showing clear signs of growth (which can be rapid over the early instar period) and feeding (e.g. green tissue visible in their digestive tract and frass being produced). Buds were examined under the microscope for signs of larval feeding, and after the five day period were dissected to check for larvae which may have made their way deep into the internal tissue.

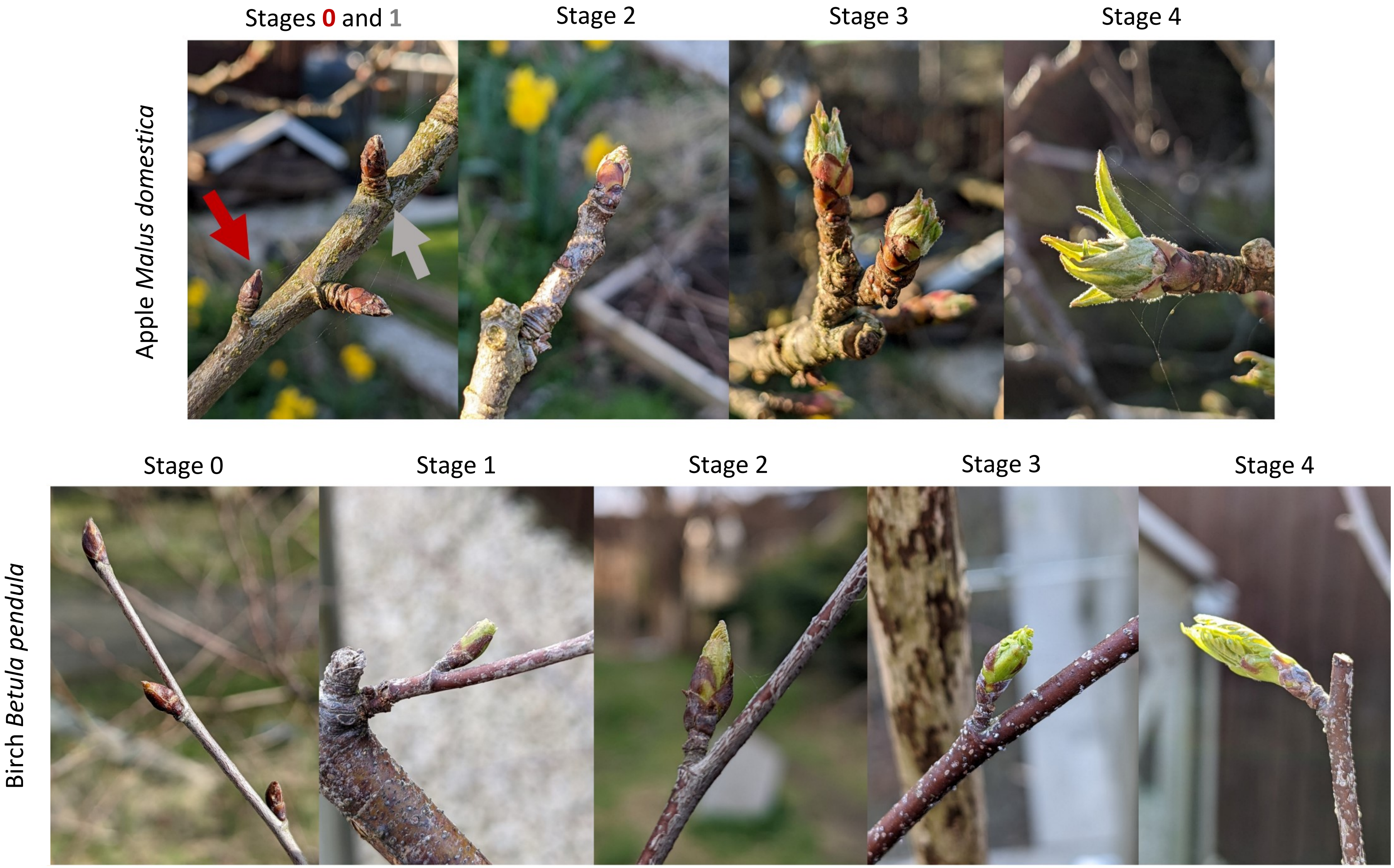


Figure 4.1. Stages of bud development across a selection of deciduous trees. See Table 2 for a description of each stage.

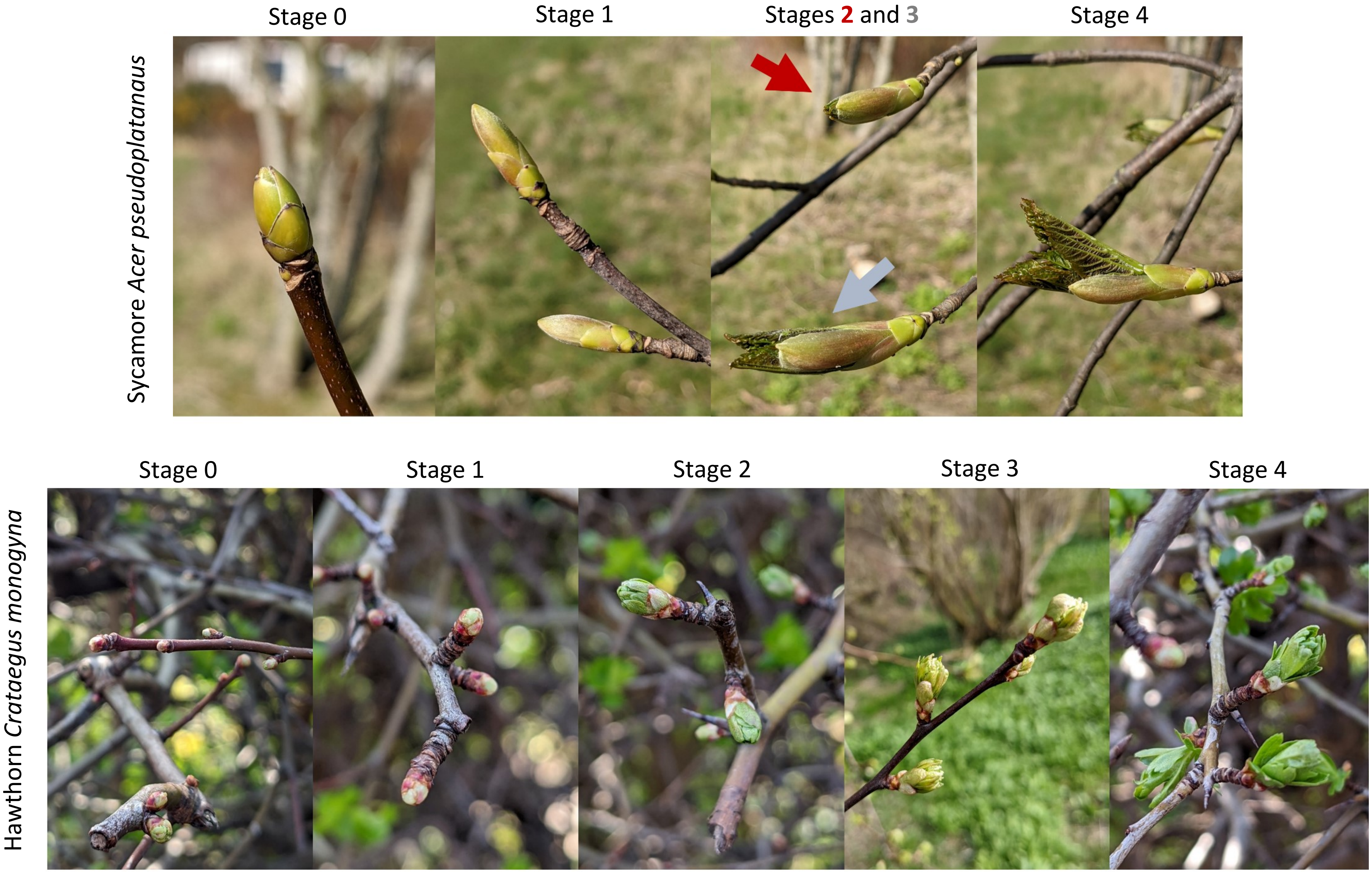


Figure 4.1 *cont*. Stages of bud development across a selection of deciduous trees. See Table 2 for a description of each stage.

4.3.4. Statistical analyses

All statistical analyses were conducted in the *R* v. 4.0.3. Bayesian mixed model package MCMCglmm (Hadfield, 2010). The overall duration of caterpillar survival (in days) when starved was modelled using a general linear mixed model. Between species and between temperature treatment effects were tested, and any among-caterpillar species differences in the effect of temperature treatment was tested by including an interaction term (Model 1. Response: Individual Survival Time; Explanatory Fixed effects: Caterpillar species, Temperature Treatment, Caterpillar species:Temperature treatment; Random effect: Rearing Culture).

Survival *across time* when starved was modelled using a binomial generalised linear mixed model—this allowed me to test for differences in the rate of mortality. I included day to test for an effect of time on probability of survival, and interactions between species and temperature treatment to determine how the slope this relationship varied across these treatment groups. To determine if there were among-species differences in the effects of temperature on the slope of survival across time, I included a three-way interaction between day, species and temperature. Inspection of the data revealed that the pattern of survival across time was likely to be quadratic, so I included a quadratic effect of day and allowed this to vary with species and temperature treatments (Model 2. Response: Individual Survival; Explanatory Fixed effects: Day, Day:Species, Day:Temp, Day:Species:Temp, Day^2, Day^2:Species, Day^2:Temp, Day^2:Species:Temp; Random effect: Rearing Culture).

Probability of establishment on buds of different stages was modelled using a binomial generalised linear mixed model. To test for an overall effect of bud stage this was fitted as a fixed term in the model. To determine whether probability of establishment varied across host-plants, I fitted this as a random term, and included an interaction between host-plant species and bud stage to determine if the effects of bud stage on average varied across host-plants (Model 3. Response: Individual Establishment; Explanatory Fixed effect: Bud Stage; Random effects: Rearing Culture, Host-plant Species, Host-plant Species:Bud Stage). To estimate the variance components of bud utilisation, Model 3 was re-run with all effects fitted as random terms (Model 4. Response: Individual Survival; Random effects: Bud Stage, Rearing Culture, Host-plant Species, Host-plant Species:Bud Stage). Variance components were then estimated as percentages on the link scale.

All models were run across 1.5 million iterations, with a burn-in of 500000 and thinning every 100 iterations. In Models 1 and 2, rearing culture was included as a random term to control for systematic differences introduced by slightly different rearing environments. Models used default priors for the fixed effects (mean = 0, with a large variance), inverse Wishart priors on the residual (though this was fixed in the binomial bud model), and parameter expanded priors for the random effects.

4.4. Results

4.4.1. The effects of temperature on starvation tolerance

For caterpillars held at 5°C, the duration of survival when subject to starvation ranged from 5.99 days (95% credible intervals [CIs]: 4.25, 7.77) in *E. defoliaria* to 27.60 days (CIs: 25.80, 29.34) in *L. monacha.* Increased temperature significantly, and consistently, decreased the tolerance of starvation across all species (Figure 4.2), though the magnitude of this effect varied markedly (see, for example, *L. monacha*). When held at 21°C, the duration of survival ranged from 1.13 days (CIs: 0.00, 2.90) in *O. brumata* to 6.11 days (CIs: 4.33, 7.84) in *L. monacha* (see also Appendix 1, Tables S4.2 and S4.3).

Patterns of caterpillar survival across time conformed well to a classic sigmoid shape, though some less steep than others (e.g. *L. monacha* maintained relatively constant levels of survival for up to 20 days, followed by linear declines to approximately 100% mortality by 40 days) (Figure 4.3). Relative to the slope of survival probability of the winter moth at 5°C (the reference level; -14.87, CIs: -28.07, -2.08) only that of the black arches declined at a significantly lesser rate (14.68, CIs: 2.09, 28.12).There was no significant difference between the slope of winter moth at 5°C and that at 21°C (-67.52, CIs: -163.39, 43.26) (see also Appendix 1, Table S4.4).

4.4.2. The ability of neonate winter moth caterpillars to exploit developing host buds

Winter moth caterpillars showed an ability to utilise buds of all stages (1-4) to some extent, with the probability of establishment on any given bud increasing with increasing developmental stage (Figures 4.4 and 4.5). Typically, across species, the probability of establishment was significantly different between Stage 1 and Stages 2-4, though not

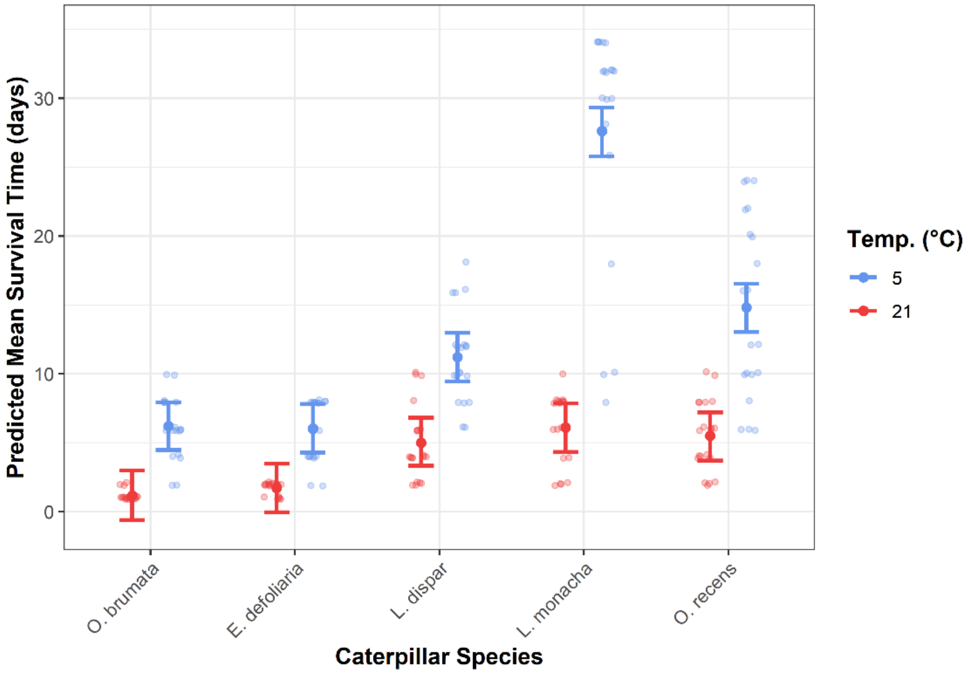


Figure 4.2. The effects of temperature on time until death when starved (mean estimate ±95% CIs) for neonate caterpillars of a selection of spring-feeding caterpillars. Smaller, pale points show horizontally jittered raw data of the starvation tolerance of each individual caterpillar. Increased temperature decreases mean survival time across species, though the effects vary in magnitude.

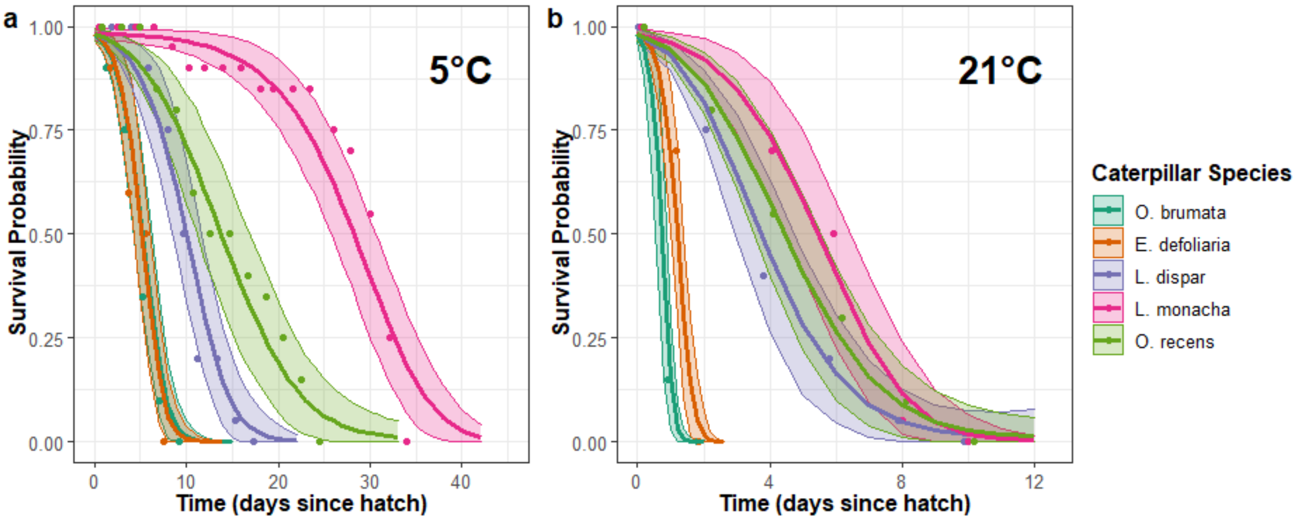


Figure 4.3. Changes in the survival probability across time of spring-feeding neonate caterpillars when starved, housed at (a) 5°C and (b) 21°C. Lines show mean (with 95% CIs) estimates of probability of survival across time. Points show jittered raw data of mean survival in each treatment group on each day when this was measured. Data was jittered to make cluttered points in the top left portion of the graph visible.

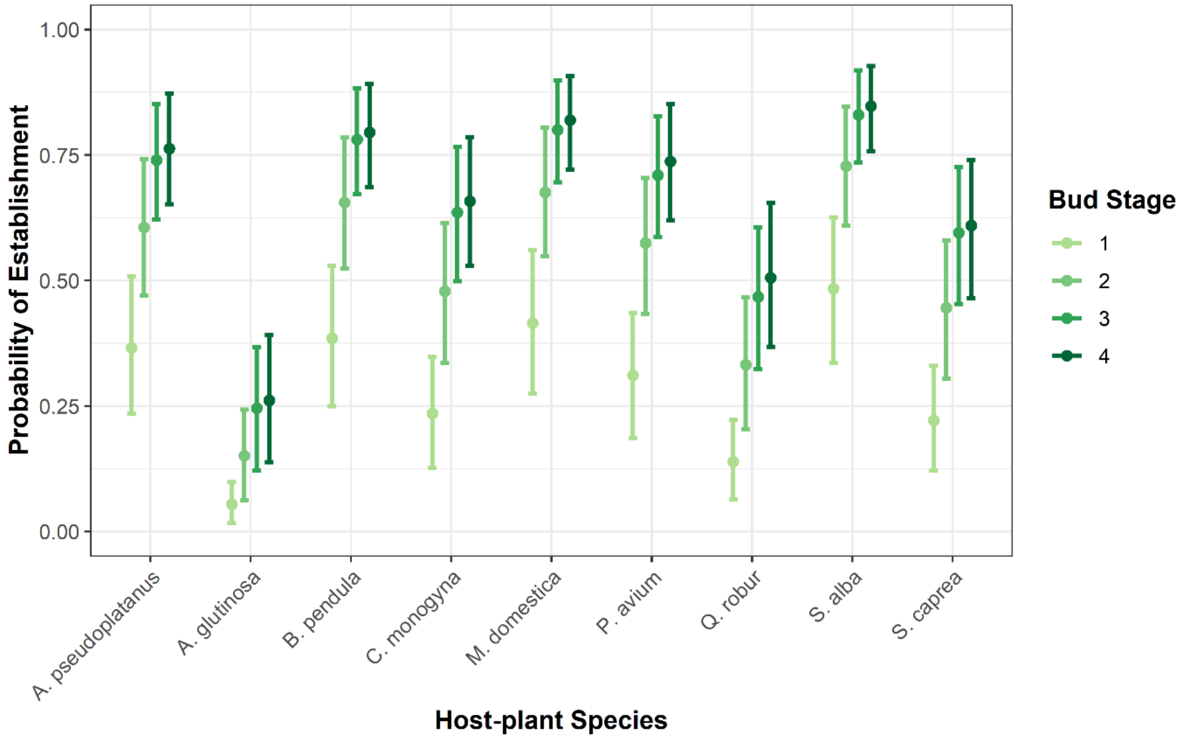


Figure 4.4. Probability (±95% CIs) of winter moth caterpillar establishment five days after hatching when placed on buds of different ages across nine host-plant species. Establishment was interpreted as caterpillars having survived the intervening period, showing clear signs of growth and feeding. Bud stages range from swollen but closed (Stage 1) to entirely open with expanding and morphologically recognisable leaves (Stage 4). Transition from Stage 1 to Stages 2, 3, and 4 appears generally to be the crucial step, causing a sudden, sizable increase in the probability of establishment, although caterpillars can apparently still utilise these very under-developed buds as food.

significantly different between Stages 2-4. For example, in birch, mean probability of survival increased from 0.38 (CIs: 0.25, 0.53) at Stage 1, to 0.66 (CIs: 0.52, 0.78) at Stage 2, 0.78 (CIs: 0.67, 0.88) at Stage 3, and 0.79 (CIs: 0.69, 0.89) at Stage 4. Host-plant species explains almost as much variation as bud stage in the probability of establishment, while the host-plant:bud stage interaction explained very little (Figure 4.6). This suggests that while both bud stage and host-plant species are important determinants of caterpillar establishment, the effect of bud stage did not vary significantly across host-plants (see also Appendix 1, Table S4.5).

4.5. Discussion

I found that the mean duration of survival for caterpillars when subjected to starvation varied considerably across five spring-feeding species, ranging from days to weeks. Survival across

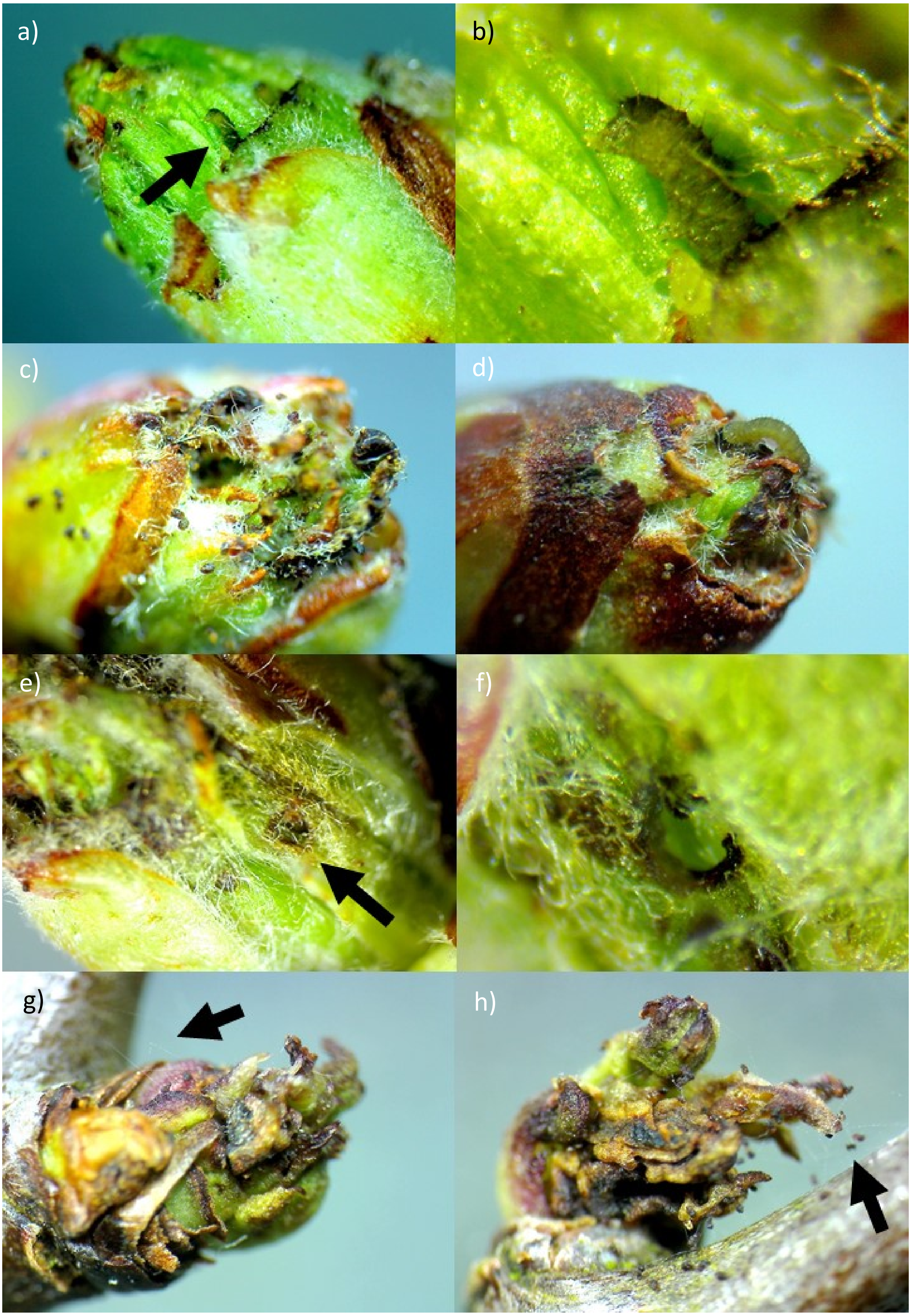


Figure 4.5. Caterpillars of the winter moth exploiting buds of apple *Malus domestica* (a-f) and hawthorn *Crataegus monogyna* (g-h) at varying stages of development. (a-b) Caterpillar feeding on the tissue of developing leaves while taking cover under an adjacent bud scale. (c) Larval feeding damage (a hole bored into the apex of

the bud) surrounded by frass showing continued feeding. (d) Caterpillar feeding on a tiny area of green plant tissue exposed at the apex of a bud, bud scales still tightly closed. (e) A hole bored into the side of an expanding bud (black arrow, and close-up in [f]). (g-h) Feeding damage, frass, and silken webs spun by feeding larvae on developing buds, indicated by arrows.

time when starved showed a classic sigmoid pattern. This, and similar trends reported by other studies (Wint, 1983; Hunter, 1990, 1993; Tikkanen and Julkunen-Tiitto, 2003), implies inter- and intraspecific variation in starvation tolerance of a considerable degree, in contrast to the findings of Reavey (1992), for example. Caterpillars of the winter moth, in apparent contrast to many of assumptions made in the literature (Table 4.1), showed a considerable propensity to utilise the unopened and opening buds of many host-plant species. The key turning point in bud development (from the point of view of larval utilisation) does indeed appear to be it starting to push open and outward, due to the growth of the young leaves inside (Stages 2 onwards, see Figures 4.1 and 4.4). Prior to this point, however, caterpillars still show an ability to feed on the underdeveloped buds, albeit much reduced. In addition, higher temperatures were found to significantly decrease the ability of all species to tolerate starvation, reducing their survival time often by a large margin (Figure 4.2). This is consistent with trends identified in the literature (see Section 4.5.1). When held at 21°C, there was far less variation between species in survival time—winter moth and the mottled umber survived for significantly less time when starved than the remaining three species, though the magnitude of this difference was not great (~2 vs ~5 days).

4.5.1. Starvation tolerance

The results of this study largely accord with the generally less systematic and more anecdotal evidence presented in the wider literature for the winter moth. Survival has been found to extend to over a week at lower temperatures, declining precipitously over a day or two at higher temperatures (Patocka, 1972; Wint, 1983; Hunter, 1990; van Asch *et al.*, 2007). Tikkanen and Julkunen-Tiitto (2003), who quantified time in degree days rather than calendar days, found over 70% mortality in winter moth with an exposure of 33dd (for individuals held at 10.5°C), approximately 3 calendar days, which fits fairly well with expectations based on the results presented here, and elsewhere (e.g. Mitter e*t al*. [1979] in Long Island, New York).

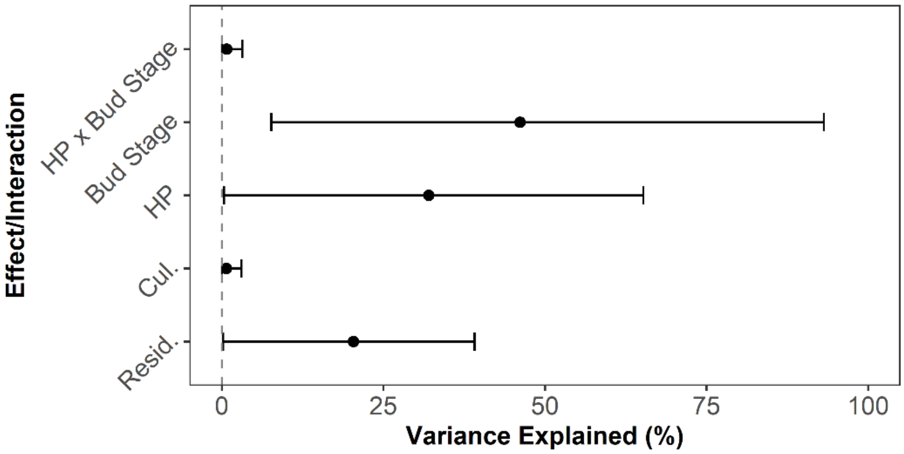


Figure 4.6. Variance components (mean ±95% CIs) of the effects of bud stage and host-plant on probability of winter moth caterpillar establishment, estimated on the link scale. The interaction between bud stage and host-plant species accounts for very little of the variation in the data, suggesting that the effects of bud stage on probability of establishment are not significantly different across host-plant species.

Cuming (1961) stated that winter moth caterpillars could survive up to five days without food, which we would expect at a mean ambient temperature of around 8-10°C (Wint, 1983; Hunter, 1990). Overall, it is interesting to note that, paradoxically, the winter moth, despite being perhaps the most consistently abundant and widespread species considered in this study, displays among the lowest tolerance to starvation.

Among caterpillar species, tolerance of starvation may be influenced by a number of phenotypic attributes. For example, larval size at hatch (and throughout development) may affect susceptibility to starvation (Jones, 1977; cf. Reavey, 1992). Polyphagous species may show less starvation tolerance than monophagous species because they have the option to disperse to alternative host individuals and species (Hunter, 1990). Many neonate larvae obligately or facultatively consume their eggshell as their first meal (Friedrich, 1983) and since dietary composition is known to influence endurance during periods of starvation (Stockhoff, 1991) this could be an important biological factor. However, both the interspecific and intraspecific sample sizes in this experiment are insufficient for a formal comparative analysis of such traits. This would be an obvious direction for future research, particularly with regard to its relevance for phenological synchrony in spring-feeding species, perhaps as a meta-analysis of data extracted from the literature or a larger-scale experimental study.

This study does, however, test starvation tolerance across a suite of spring-feeding species which allows us at least to move beyond the winter moth and say something about the generality of certain patterns across these species. Indeed, of the other species included in this study, the only one for which I can find previous measures of starvation tolerance is the gypsy moth. Like the winter moth, this species is an economically important Palaearctic outbreaking caterpillars, which has been introduced to North America, and has spread rapidly there (Beadle and Leckie, 2012). Hunter (1993) found that below 10°C, gypsy moth caterpillars died at a rate of approximately 10%/day, increasing to just under 20%/day at 20°C. At these rates, survival within a sample population would decline to zero in around ten or five days, respectively. This accords fairly well with the results presented here (Figure 4.3). Earlier, less systematic studies, noted similar results (4.3 days at 25°C [Stockhoff, 1991] and approx. 4-5 days under natural conditions [De Groff, 1969; Capinera and Barbosa, 1976]), though others have suggested a far greater degree of tolerance (e.g. up to 20 days at 12°C and 25 days at 3-5°C [Patocka, 1972]).

Despite the potential significance of starvation tolerance as an adaptive mechanism for caterpillars, particularly in spring-feeding species where synchrony can strongly affect fitness, the subject has received comparatively little attention. Surveying available data on those other spring-feeding species for which this has been measured, we see a very clear continuum of starvation tolerance which fits well with the pattern evident from the species I have analysed here. At one extreme, some species can endure very prolonged periods without food, and with seemingly little negative effects. The tent caterpillars *Malacosoma* spp. (Lasiocampidae), for example, show a notable degree of tolerance to starvation, on the order of several weeks (Parry *et al.*, 1998; Abarca and Lill, 2015; Kharouba *et al.*, 2015). In the oak processionary moth *Thaumetopoea processionea*, Wagenhoff *et al*. (2013) found fairly consistent survival over 10 days under naturalistic conditions followed by a linear decline to 100% mortality after approximately 35 days. This is striking similar to the pattern displayed by the black arches in this study (see Figures 4.2 and 4.3). In the brown-tail moth *Euproctis chrysorrhoea*, we see an extreme example of starvation tolerance, even at high temperatures—this species spends up to nine months as a caterpillar, overwintering as a larva (Henwood *et al.*, 2020). At 25°C caterpillars can survive without food for up to 15 days, and in excess of 20 days at 20°C (Patocka, 1972). At the other end of the continuum, we have species with fairly low starvation tolerances, similar to that of the winter moth and mottled umber (Figures 4.2 and 4.3; Wint, 1983; Hunter, 1990). In the non-outbreaking but spring-feeding quaker moths *Orthosia* spp. (Noctuidae), caterpillars can endure only several days without food at moderate temperatures (Reavey, 1992). Similar responses are shown by the brown oak tortrix *Archips crataegana*, the red-headed chestnut *Conistra erythrocephala* (Patocka, 1972), and the fall cankerworm *Alsophila pometaria* (Schneider, 1980b).

Given the unpredictability inherent in their environment and in the availability of food, it is surprising that spring-feeding caterpillars, particularly those which we observe to be abundant in the field, do not universally have high tolerances for starvation. However, interspecific differences in starvation tolerance may reflect different adaptive strategies to deal with the problem of early spring-feeding. For example, the green oak tortrix *Tortrix viridana* (Tortricidae) is another significant spring-feeding defoliator, often found alongside the winter moth (Smith *et al.*, 2011). Caterpillars of this species can endure starvation for almost twice as long as caterpillars of the winter moth (Patocka, 1972; Wint, 1983; Hunter, 1990). The green oak tortrix is (largely) a specialist on oak foliage, and does not have the option of feeding on alternative host-plant species as the winter moth does. As a consequence, this species also shows a much reduced propensity to disperse relative to the winter moth (Edland, 1971; Hunter, 1990). Although the winter moth is more competitive during larval development (Hunter and Willmer, 1989), the green oak tortrix is often more abundant in the field (Hunter, 1992), implying that the relative heightened susceptibility of winter moth caterpillars to asynchrony (see Chapter 3)—perhaps partly accounted for by low resistance to starvation—may mean that the tortrix has a slight competitive edge in nature on oak.

Faced, upon hatching, with a dearth of available food in spring, caterpillars have a limited number of options as to how they can best expend their finite available energy supplies. Jones (1977) outlined the difference between what he called “conservative search” (searching a small, local area very thoroughly) and “radical search” (moving further afield, and searching a wider area more cursorily) in caterpillars. Conservative search is optimal where the resources the insect requires are expected to be close by and radical search is more suited to situations where the required resource is not expected to be close by, but is randomly distributed in the environment. These two strategies reflect the differing approaches taken by the green oak tortrix and winter moth (Hunter, 1990), and, in this case, might offer at least a partial explanation of differences in their degree of starvation tolerance.

Although for young, neonate caterpillars, the ability to resist starvation would seem to be an obvious and highly effective mechanism to aid survival, particularly in unpredictable or variable environments such as a spring woodland, it may not be entirely without cost, and larval fitness and behaviour might be affected later in life by having endured a period of starvation (Abarca and Lill, 2015). Starvation can also serve to induce other behaviours which promote food-finding (Jones, 1977; Wint, 1983)—in the winter moth, the absence of food promotes dispersal in young larvae (Holliday, 1977). Capinera and Barbosa (1976), in their own trials of larval starvation tolerance, noted that caterpillars typically become inactive long before they actually die—of much more significance then, than simply survival, was the period across which they remained sufficiently healthy and active enough to continue to search for a new, more suitable location and host. In this experiment, I attempted to rectify this problem by recording "survival" only where caterpillars showed a clear movement response to external stimulus (see Section 4.3.2).

4.5.2. Feeding on buds

The results of these experiments conflict somewhat with the typically adopted view in the literature on mismatch in the woodland caterpillar system, which assumes that early hatching caterpillars are unable to exploit buds before they have broken (Table 4.1). I found that neonate winter moth caterpillars could begin to feed on buds which are swollen but not yet open, albeit with a lower level of success than on opening and open buds (Figures 4.4 and 4.5). This is not, however, a new observation—many species of insects, including Lepidoptera (Langmaid *et al.*, 2018), attack developing plant buds (Schoonhoven *et al.*, 1998). The caterpillars of the British hairstreak butterflies, for example, feed in early spring, and commence their larval development by burrowing into flower and shoot buds, sometimes feeding exclusively or preferentially within these structures until they are too big to do so (Eeles, 2019). It is widely reported in entomological literature that, when rearing a range of species in captivity, where caterpillars have hatched too soon they can be fed on unopened buds that have been cut in half and provided to the young larvae (e.g. Dickson, 1976; Friedrich, 1983; Cribb, 2001).

Even within the tree/winter moth study system, particularly outside of the main body of literature dealing with the MMH, there are numerous accounts of winter moth caterpillars hatching too early but burrowing into unopened buds to feed (Stokoe, 1948b; Porter, 2010) (Table 4.1). Part of this apparent inconsistency could be accounted for by the attempts among various authors to impose a dichotomous classification on a continuum of bud and leaf development. Furthermore, the morphology of buds, their developing morphology across time, and their relative phenology, all vary considerably across host-plant species (Figure 4.1). The fate of a newly hatched caterpillar is therefore as much affected by the taxonomic identity of the tree on which their mother happened to find herself for oviposition as it is by their degree of synchrony with that individual host-plant—this is borne out strongly by the results presented here (Figure 4.6).

I deliberately adopted a classification of bud development which identified stages that might be functionally different for caterpillars, so that it could be applied across host-plant species. The fact that the interaction between bud stage and host-plant accounts for very little of the variation in probability of establishment (Figure 4.6) suggests that the effect of bud stage is fairly consistent across species, vindicating this approach. As such these stages do indeed seem to represent meaningful steps in bud development and this classification would seem to be a good reflection of the ability of caterpillars to exploit each stage. It should be borne in mind that tree species and individuals will likely not proceed through these stages at similar rates. Such variation will extend or contract the duration of each period, introducing a great deal of heterogeneity, at the population level, in their relative suitability for consumption by young caterpillars. Quantifying the degree of variation in the availability of plant material across spring time, and how this varies across host-plant species, populations and individuals, would be an important next step in understanding the complex nature of the environment which caterpillars face in spring. This will necessitate a greater understanding of how the morphology of overwintering and developing buds functions, across species, to deter herbivory, and how insects can overcome these defences and attack them.

Interspecific heterogeneity among hosts is particularly important since almost all the previous literature considering the MMH operating within the winter moth system focuses on a single host-plant species, English oak *Quercus robur*. In fact, oak may be an unusually difficult species to feed on, with a particularly broad range of anti-predator defences, precisely because it is host to such a large number of insect herbivores (Southwood, 1961; Kennedy and Southwood, 1984; Strong *et al.*, 1984), many of them specialists on oak. In this experiment, probability of establishment was indeed unusually low on oak (Figure 4.4), highlighting the likely importance of other host-plant species for winter moth caterpillars in the field, and the problem with adopting a focus on any one resource species in the life history of a polyphagous consumer.

4.5.3. Buffered against early hatching

In contrast to the view typically adopted in the literature (e.g. Table 4.1) that hatching before bud-burst occurs on their host species is greatly deleterious, if not fatal, the caterpillars of spring-feeding moth species can show a considerable tolerance of starvation while they wait for food to become available. Further, the winter moth—a species with small, fragile larvae—is able to exploit unopened and opening buds as food. Indeed, some spring-feeding species have been shown to hatch consistently *before* bud-burst in the field (Wagenhoff *et al.*, 2013) and can even be largely resistant to any negative effects of asynchrony (Kharouba *et al.*, 2015). Alongside the considerable potential of many caterpillar species to disperse to another host-plant (Fitzgerald, 1995; Bell *et al.*, 2005), these traits and behaviours—combined to various degrees, or in isolation—could clearly serve as adaptive mechanisms to significantly buffer individuals against the negative effects of early hatching. For example, in the green oak tortrix (an oak specialist, Hunter, 1990; though see Maitland Emmet and Heath, 1992; Young, 1997; Sterling *et al.*, 2012) the mean duration of larval starvation tolerance matches fairly well the phenological variation in their host-plant (Ivashov *et al.*, 2002), highly suggestive of mismatch operating as a selective driving force for the evolution of that high degree of tolerance. Similarly, Tikkanen and Julkunen-Tiitto (2003) found that starvation tolerance in the winter moth matched variation in host bud-burst timing and also the temporal extent of tolerance of late foliage. It should not necessarily be surprising that insects being thrust into an uncertain, variable environment have mechanisms to cope with this. A puzzle, however, is why the winter moth—a highly successful, abundant, pest species—was comparatively a poor performer in the starvation trials. Van Asch *et al.* (2007) reason, from the fact that 90% of winter moth caterpillars die of starvation after five days at 12°C, that eclosing five days prior to bud-burst would mean that the mean fitness of an individual caterpillar would decline to almost zero. For a trait under such seemingly strong selection, however, hatching date displays considerable variation—eggs kept under identical conditions can hatch across a 28-day time period (Buse and Good, 1996). Lower average temperatures would obviously extend this period, so the supposition that caterpillars will quickly starve is geographically (and perhaps microclimatically) contingent, but also ignores the ability of the caterpillars to feed on unopened buds—this would further extend the window of survival. It may also be that the ability of winter moth caterpillars to exploit early, developing buds exceeds that of other species, such that the need to tolerate starvation is lessened. Whatever the evolutionary explanation, the ecological situation is clearly not a simple black and white story of synchrony or asynchrony, match or mismatch.

Chapter 5: The effects of early leaf maturation on the survival and growth rate of winter moth *Operophtera brumata* caterpillars

5.1. Abstract

Spring-feeding arboreal caterpillars must time their appearance in spring to match the availability of young, under-defended foliage. Caterpillars which hatch later suffer reduced fitness as they are forced to feed on more mature, less palatable plant material. However, it is unclear at what point in development the biochemical and structural effects of leaf maturation impact caterpillar fitness. It has been argued both that the highest mortality occurs in the early stages of caterpillar development, and that it is the accumulation of defensive chemicals much later, as caterpillars are approaching pupation, that provides the selective pressure for mismatch. In addition, previous assays of caterpillar performance have tended to focus on one of a limited range of metrics, such as survival, size attained, or development time, which could offer a skewed perspective of fitness. Here, I used foliage collected at two time points in the field soon after bud-burst, on three host-plant species, to determine more precisely when foliage begins to become unpalatable. I tested performance across caterpillar species, and quantified variance in performance between individual trees of the same species and among caterpillar broods. I found that overall survival was higher on birch *Betula pendula* than on oak *Quercus robur* or sycamore *Acer pseudoplatanus.* Growth rate was higher on oak, but development time was shorter, suggesting a potentially compensatory interaction. There was no substantial effect of leaf age on performance, suggesting that leaf development on these host species during the two week period across which they were sampled did not affect their palatability to caterpillars, consistent with the idea that changes in foliage later in development affect caterpillar fitness. Furthermore, there was considerable variance in caterpillar performance among broods and among individual host trees, which could act as a buffer against trophic mismatch.

5.2. Introduction

Where the occurrence of a consumer and its resource taxa are temporally synchronised, divergent phenological responses to climate change can lead to trophic asynchrony, with potentially negative fitness consequences for individual consumers and their populations (Hjort, 1914; Cushing, 1969, 1990; Durant *et al.*, 2007). A classic model system for this phenomenon is spring-feeding woodland caterpillars and their host-plants, particularly the winter moth *Operophtera brumata* and English oak *Quercus robur* (e.g. Hunter and Elkinton, 2000; van Asch and Visser, 2007; van Asch *et al*., 2007, 2012; Singer and Parmesan, 2010; Burgess *et al.*, 2018; Shutt *et al*., 2019; Samplonius *et al.*, 2020; see Table 3.1). As discussed in Chapters 3 and 4, fitness in winter moth caterpillars is generally thought to depend on a very high degree of phenological synchrony between the timing of caterpillar hatch from their eggs and the timing of bud-burst on their host tree. Any mistiming, even of just a few days, may exert significant negative effects, leading to trophic mismatch and a reduction of individual fitness (Tikkanen and Julkunen-Tiitto, 2003; van Asch *et al.*, 2007).

The speed with which host-plant foliage becomes unpalatable to these caterpillars has been ascribed to the rapid rate at which it appears and matures in spring time. Hatch too early, before the leaves have appeared, and caterpillars are without food and can rapidly starve (Cuming, 1961; Wint, 1983; Tikkanen and Julkunen-Tiitto, 2003). Hatch too late and the foliage quickly becomes unpalatable for young caterpillars due to structural and biochemical changes, such as leaf toughening and the accumulation of noxious secondary chemicals, e.g. tannins (Feeny, 1968, 1970; Tikkanen and Julkunen-Tiitto, 2003). For the caterpillars of the winter moth, therefore, hatching later, when foliage is certain to be abundant, is not a safe and reliable strategy (cf. Singer and Parmesan, 2010). Caterpillar survival when neonate or in the earliest instars is very variable, and it has been suggested that the greater part of mortality in any given treatment group results from the failure of first instar larvae to establish themselves on a given host-plant (Varley *et al.*, 1974; Wint, 1983). Caterpillars of spring-feeding species, including the winter moth, therefore appear to be specialised to exploit the narrow phenological niche during which young host-plant foliage is poorly defended.

In Chapter 3, I manipulated the timing of caterpillar hatch in a number of spring-feeding species to simulate degrees of late hatching asynchrony and measured the effects across a number of performance metrics. Although this experiment allows us to say something about the fitness effects of late hatching, caterpillar development occurs over a period of 20-30 days (see Chapters 2 and 3) and as such it is difficult to use these data to pinpoint the precise period over which foliage becomes less palatable—individuals hatching five days late, for example, may have reduced survival, but it could be changes in foliage palatability that take place much later in the larval period that result in that reduced rate of survival. This is important because if caterpillars can recognise the host-plant that they are on and that the foliage is likely to become unsuitable for them soon, they may be able to hasten development (Kirsten and Topp, 1991; Stamp and Casey, 1993; Kerslake and Hartley, 1997) or disperse to a new site with more favourable conditions (Edland, 1971), for example.

In his classic work on this system, Feeny (1970) investigated the effects of late hatching by feeding captive-reared fourth instar winter moth caterpillars on oak foliage collected in the field on two separate dates, two weeks apart. Foliage from each collection was frozen at -20°C and provided to the captive larvae. He found that caterpillars fed on the younger foliage were much heavier (30mg) than those fed on older foliage (10mg), which would translate to a large difference in adult fecundity (see Chapters 2 and 3, and Appendix 2). From this, Feeny argued that mistiming with respect to bud-burst could be detrimental for caterpillars, but that these effects would only manifest themselves at the end of the larval feeding period; that this was the crucial period during which foliage became unsuitable for caterpillars: "[i]t is concluded that some change or combination of changes occurs in the oak leaves over a period of only 2-3 weeks in late May which has a markedly adverse effect on the larval growth rates, pupal weights, and adult emergence of the winter moth" (p 569; Feeny, 1970).

There are several reasons, however, to remain somewhat cautious of the implications of Feeny's study, despite its widespread citation (see Table 3.1). For instance, foliage from a single host tree on two calendar dates was used as food but individual trees can vary greatly in their baseline secondary chemistry, biomechanical properties, and the rates at which they mature (Suomela *et al.*, 1995; Henriksson *et al.*, 2003; Tikkanen and Julkunen-Tiitto, 2003; Laitinen *et al.*, 2005; Peltonen *et al.*, 2010; Gaytán *et al.*, 2022)—we may then be seeing only the idiosyncratic performance effects of timing on this particular tree. In Feeny's experiments caterpillars were also initially reared on the same diet before switching onto old or young frozen foliage, and there is good reason to suppose that diet switching during development can at least sometimes be detrimental (Dickson, 1976; Friedrich, 1983; Cribb, 2001; though cf. Johns *et al.*, 2009). Indeed, if caterpillars are able to detect gradually accumulating anti-herbivory defences in plant material and then exhibit plastic behavioural or physiological changes in response to ameliorate these effects, the sudden and unexpected diet change may prevent this process taking place and could account for the substantial difference in performance between the two treatments.

A further limitation both in the literature on the MMH in spring-feeding caterpillars and my own experiments (Chapter 3) is a bias in terms of the metrics used to quantify caterpillar performance. Necessarily, the number of things which can be measured in any experiment is limited. Probability of survival to pupation and final pupal mass—strongly correlated with fecundity in females (see Appendix 2)—are the most frequently used metrics of caterpillar performance in the literature (Figure 5.1). However, these measures are generally made under lab conditions, where the only factor affecting fitness is the palatability of the host-plant material. Conditions in the field may not necessarily be equivalent to those in the lab, and a range of other factors may come into play that could affect fitness. For example, if caterpillars pupate more quickly, at a smaller size, then the resulting adults will have reduced fecundity—however, if caterpillars in the wild are more vulnerable to parasitism, predation, or adverse environmental conditions than pupae, then reducing development time could, at the same time, result in a reduction in exposure to these other extrinsic sources of mortality. Quantifying growth rate over time could therefore provide us with additional insights into how these different factors might interact to contribute to overall fitness in the field.

Here, I consider in more detail the fitness effects of early leaf development in three host-plant species on winter moth caterpillars. Adopting a similar method to Feeny (1970), I reared caterpillars on frozen foliage collected over a two week period to test whether leaf maturation during this time window affects palatability and caterpillar performance. To emphasise the potentially confounding role of using a small number of host trees, I examined variation in caterpillar performance between individual trees and across broods. I discuss the significance of this variation in light of asynchrony, and how it may contribute to buffering populations against environmental uncertainty, the unpredictability of spring, and future climate change. In contrast to most studies, which consider overall caterpillar performance, I quantified performance throughout development. I tested whether overall survival differed

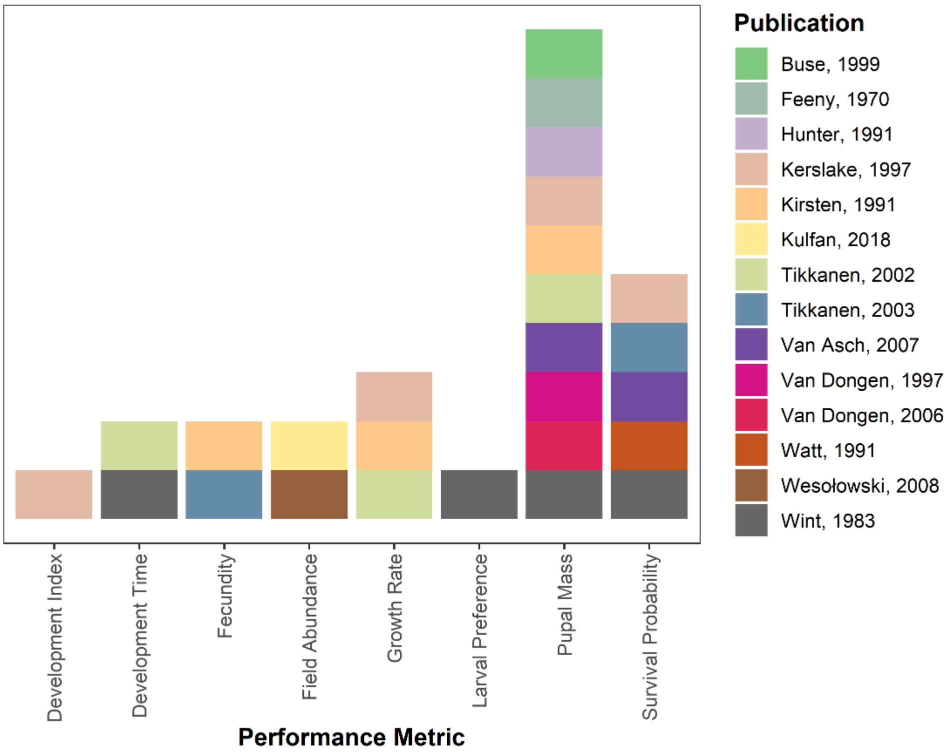


Figure 5.1. The frequency of different performance metrics used to quantify the effects of trophic asynchrony on winter moth caterpillar fitness in the literature. Publications listed by first author. There is a clear skew towards pupal mass and probability of survival to pupation. Definitions of each metric: Development Index, a bespoke measure of rate of growth described by Kerslake; Development Time, days to pupation from hatch; Fecundity, number of eggs laid by adult female; Field Abundance, the abundance of winter moth caterpillars in the field, usually beaten from host trees; Growth Rate, various measures of mass accumulation across time; Larval Preference, caterpillar preference for a particular host-plant species; Pupal Mass, (typically) fresh mass of pupae after feeding period; Survival Probability, probability of survival from egg hatch to pupation.

between host-plant species and foliage of different ages, as well as how rates of morality and growth change across time in these different groups. I consider how, as caterpillars grow, they may be better able to cope with the effects of leaf maturation. Using measures of growth rate and development time, I evaluate how the two might interact and discuss how shifts in one may be compensated for by changes in the other. I also briefly consider different ways of measuring caterpillar growth across time, and their relative utility and practicability for experiments such as this one.

5.3. Methods

5.3.1. Obtaining livestock

Female winter moths were collected using funnel traps designed to intercept them as they ascended tree trunks in order to lay eggs in the canopy (see Appendix 9). Traps were deployed for 36 nights in late November and December 2018 at the Hermitage of Braid Local Nature Reserve in Edinburgh, United Kingdom. Moths were trapped at two sites in the LNR: (i) a mixed stand of deciduous species, e.g. alder *Alnus glutinosa*, birch *Betula pendula*, sycamore *Acer* (55.9246°N, -3.1888°N, 60 traps); and (ii), an area almost exclusively of oak *Quercus robur* (55.9194°N, -3.1970°N, 20 traps). Several traps were fixed to tree trunks at approximately 1.5m from ground height in sufficient numbers so as to cover an area of approximately one third of the trunk circumference.

A total of 13 females were collected during the trapping period and placed individually in sealed plastic specimen tubes held at 5-7°C and in complete darkness using a Russell Hobbs RHCLRF17 table-top refrigerator. A square of moistened, crumpled paper tissue was provided to each as a laying medium. Females laid at a relatively constant rate, and eggs were periodically removed and new tissues were provided to stimulate further laying, until the death of each individual female. Eggs were removed and kept chilled at 5-7°C in petri dishes until spring.

On 14 May, the dishes of eggs were removed from refrigeration and kept at room temperature (~20°C) to stimulate maximum egg hatch (Hibbard, 2014; Hibbard and Elkinton, 2015). From the original 13 females, 8 laid fertile eggs (of varying brood sizes), yielding a total of 264 ova. Of these, approximately 190 (72%) hatched and 165 were included in this experiment. As they hatched, larvae (no more than 24 hrs old) were assigned sequentially to six treatment groups (Figure 5.2)

5.3.2. Treatment groups

In the spring of 2019, samples of foliage from three common deciduous tree species utilised as host-plants by the caterpillars of the winter moth were collected at the Hermitage of Braid LNR. Leaves were collected from 10 individual trees of *Acer pseudoplatanus*, *Betula pendula*, and six individuals of *Quercus robur* on 30 April 2019, and again from the same trees on 12

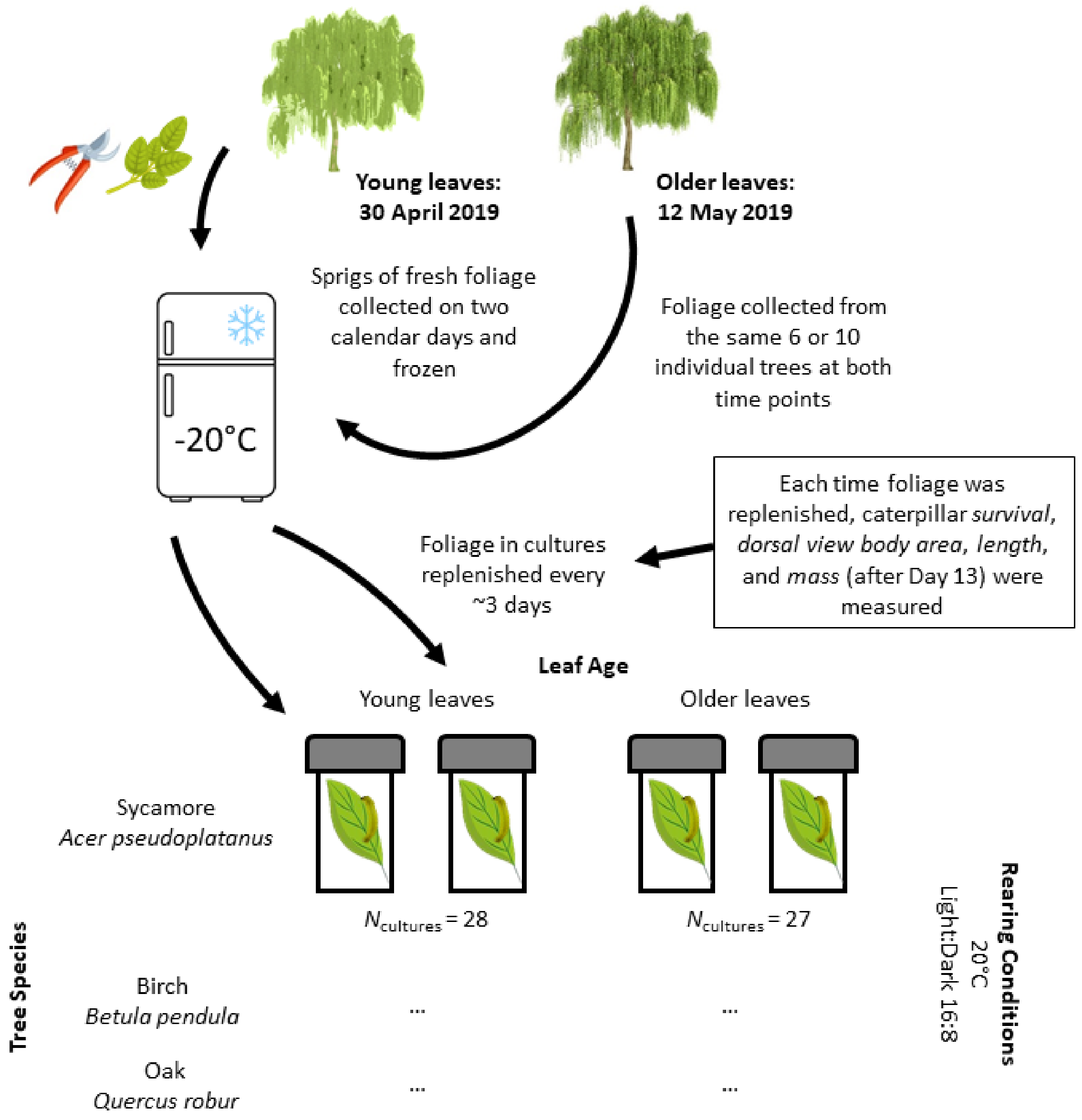


Figure 5.2. Schematic of experimental design for Chapter 5. Caterpillars were reared individually to pupation on foliage of one of two age groups, which was collected in the field and frozen. To determine if the palatability of the foliage had changed in the interval between the two leaf collection points, caterpillar performance was assayed by measuring survival and quantifying growth throughout the developmental period. Young leaves were collected when small, at around the time of bud-burst and as the developing leaves were beginning to expand. Older leaves were collected 13 days after the younger leaves.

May 2019 (Figure 5.2). The first leaf collection point was timed so as to coincide with bud-burst (Bud Stage 3 in Chapter 4, see Table 4.2) on average, across the different species and individuals. Leaf collections therefore represented a sort of cross-section of the host-plant population at each time point, and encapsulated some between-species and between-individual differences in the rate of phenological development across potential host-plants in the field in spring. Plant material was stored in sealed plastic bags and frozen at -20°C on the day of collection. Neonate caterpillars were hatched simultaneously and assigned to one of six treatment groups, “young” leaves (collected on 30 April) and “older” leaves (collected thirteen days later on 12 May) from each of the three host-plant species (Figure 5.2). Throughout their development, each caterpillar was supplied with leaves from the same individual host tree. Twenty-eight individuals were assigned to young leaves of each host-plant species and twenty-seven to old leaves of each.

5.3.3. Rearing methodology and measuring performance

Caterpillars were reared individually in glass phials to minimise variation in mortality due to factors such as the contraction of disease which might spread through close proximity (Figure 5.2). Individual cultures were stored at 20°C in a 16:8hr light/dark regime, creating relatively naturalistic conditions given the location of their source population. Approximately every three days, survival was recorded, larvae were photographed directly above using a Sony DSC-W800 camera and, from day 13, individual mass was directly measured using a Mettler AJ50 balance. Each time, a new batch of leaves were removed from the freezer, thawed, and the food in each culture was replenished. Strict hygiene practices were observed throughout—the rearing tubes were routinely cleaned and sterilised with 70% ethanol, as were any instruments used for handling.

Measuring caterpillar growth throughout their development can be difficult. Mass is a good predictor of adult fecundity in females and is therefore a useful metric of performance (see Appendix 2). However, immediately after eclosion, caterpillars weigh less than 0.001 g, making it very difficult to accurately quantify their mass at that stage. In order to measure growth from hatching I processed the photographs taken of each caterpillar throughout its development in ImageJ (Schneider *et al.*, 2012) to measure the length of larvae and the “dorsal-view area” (the body area visible from directly above, see Figure 5.3).

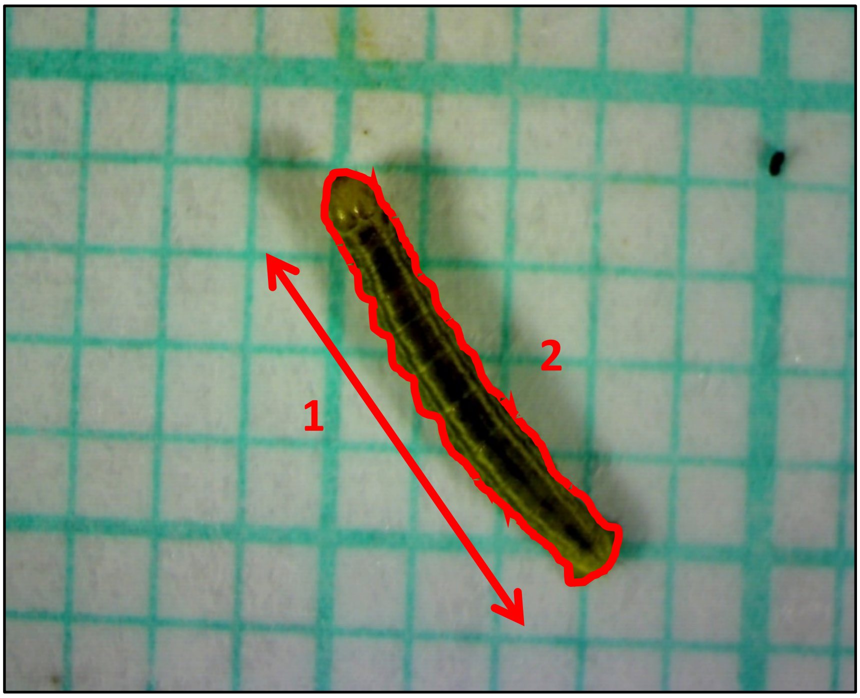


Figure 5.3. Quantifying larval development. Growth was measured as (1) length and (2) 'dorsal view area', i.e. the area of the caterpillar's body as visible from directly above. In addition, after day 13 the mass of each caterpillar was directly quantified. Scales were calculated for each photograph using the 1mm^2 background grid. Images were analysed in ImageJ.

5.3.4. Statistical analysis

5.3.4.1. Identifying an optimal measure of larval development

To test the effectiveness of caterpillar length and area as measures of development and determine which to use for subsequent analyses, I modelled their association with caterpillar mass in the latter period of development, where mass was directly measured (see Section 5.3.3). Mass is a reliable predictor of fecundity for adult females, and is therefore a good measure of fitness (see Appendix 2). I used linear models in *R* v. 4.0.3 to determine the relationship between caterpillar area and mass (Models 1 & 2. Response: Caterpillar Mass; Explanatory Fixed effects: Area), caterpillar length and mass (Models 1 & 2. Response: Caterpillar Mass; Explanatory Fixed effects: Length), and between caterpillar length and area (Model 3. Response: Length; Explanatory Fixed effects: Area). I log-transformed various combinations of area and length with mass but this did not visually improve model fit with the data, so I decided to retain the original, untransformed data. Area and length superficially showed a quadratic relationship, so in addition I also fitted Model 3 with an Area^2 term to test for improved model fit. Results suggested that area was the best measure (see Section 5.4.1) and was used for the analyses below. This analysis was conducted to attempt to determine which metric was most useful *in practice*, as measures of growth and development, even though we expect them to correlate closely as caterpillars grow allometrically.

5.3.4.2. Overall survival to pupation and development time across host species and age treatments

To determine overall mean probability of survival from hatch to pupation in each treatment group, I ran a binomial linear model in the Bayesian *R* package MCMCglmm (Hadfield, 2010). I included a leaf age term to test for differences in survival between foliage of different ages, and a host species term to test for differences between host-plant species. Finally, I included a host by age interaction term to test for differences in the effects of age in specific host-plant species (Model 4. Response: Individual Survival; Explanatory Fixed effects: Leaf Age, Host-plant Species, Leaf Age:Host-plant Species). To determine mean development time in each group (i.e. average time in days from egg hatch to pupation) I used a Gaussian linear model with the same structure, to test for the same host-plant and leaf age effects (Model 5. Response: Development Time; Explanatory Fixed effects: Leaf Age, Host-plant Species, Leaf Age:Host-plant Species), respectively.

5.3.4.3. Cumulative survival across time and growth rate

I used a binomial generalised linear mixed model in MCMCglmm to test for an effect of host-plant species and foliage age on the cumulative probability of survival across time, i.e. on any given day this is the probability of survival up to that point. This differs from overall survival probability (the measure adopted in Chapters 2 – 4) in that it describes differences in the rate and patterns of mortality across time. This model included an interaction between day (time since egg hatch) and host-plant species, and between day and leaf age treatment, to test for differences in the effect of day on survival between these different treatment groups. I included a three way interaction to allow the effects of age to vary between host-plant species (Model 6. Response: Individual Survival; Explanatory Fixed effects: Day, Day:Species, Day:Age, Day:Species:Age; Random effects: Caterpillar Individual, Brood, Tree Individual).

I used a Gaussian generalised linear mixed model in MCMCglmm with a similar structure to test for an effect of host-plant species and foliage age on growth rate. Growth was measured as caterpillar area (Model 7. Response: Area; Explanatory Fixed effects: Day, Day:Species, Day:Age, Day:Species:Age, Day^2, Day^2:Species, Day^2:Age, Day^2:Species:Age; Random effects: Caterpillar Individual, Brood, Tree Individual). In this model, I also included a quadratic effect of time to better fit the shape of the raw data, accounting for the logarithmic patterns typical of insect growth (Richards and Davies, 1977; Ernsting *et al.*, 1993).

In both Model 6 and 7 the intercept was fixed because all individuals began the experiment at the same mass and probability of survival. In addition, random terms included in both models were: individual caterpillar identity; the brood from which that caterpillar was derived; and, the individual tree from which foliage was collected. The individual caterpillar term controlled for repeated measures on the same individuals. I used the estimates of among-brood and among-tree individual variance to consider the relative importance of each.

5.3.4.4. General aspects of the models and analysis

Models were designed *a priori* and were not simplified by removal of non-significant terms. In all the analyses, sycamore was selected as the reference level host-plant, and young foliage as the reference level leaf age treatment—as such, significant difference in any metric of growth or survival was determined with respect to this species. Bayesian models in MCMCglmm were run across 1.5 million iterations, with a burn-in of 500000 and thinning every 100 iterations. Gaussian models used default priors for the fixed effects (mean = 0, with a larger variance), inverse Wishart priors on the residual, and parameter expanded priors for the random effects. In the binomial survival models, residual variance was fixed.

5.4. Results

5.4.1. Overall survival and development time across host species and age treatments

Overall mean survival probability of caterpillars to pupation was significantly higher on birch (young = 0.31, 95% credible intervals [CIs]: 0.14, 0.47; old = 0.35, CIs: 0.02, 0.52), relative to oak (young = 0.14, CIs: 0.00, 0.27; old = 0.11, CIs: 0.02, 0.23) and sycamore (young = 0.04, CIs:

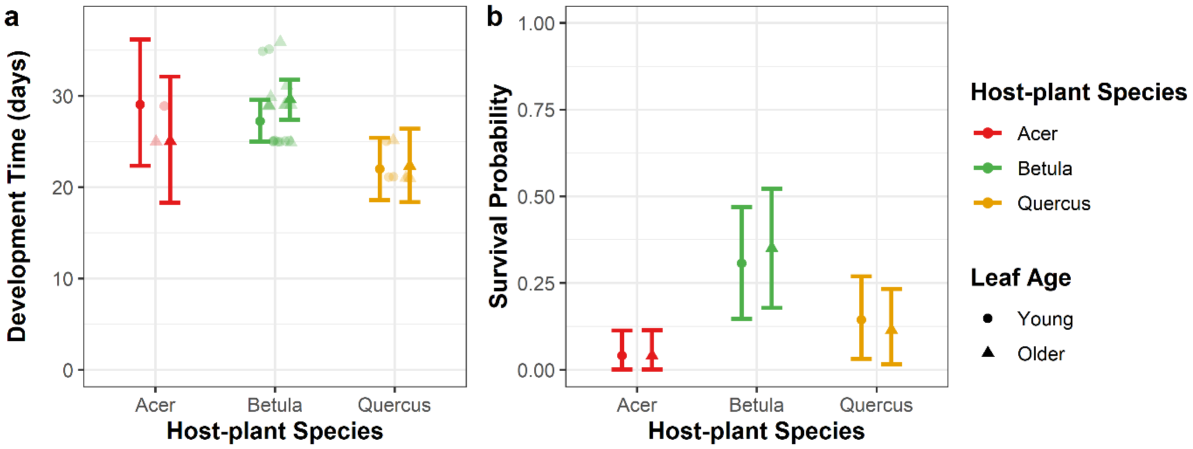


Figure 5.4. The effects of host-plant species and foliage age on overall development time and probability of survival to pupation in winter moth cateprillars (±95% CIs). Young foliage was collected at around bud-burst across the population, and older foliage thirteen days later. In (a) pale points show jittered raw data.

0.00, 0.11; old = 0.04, CIs: 0.00, 0.11). I found no significant differences in survival probability between young and old foliage across any of the species (Figure 5.4; see Appendix 1, Table S5.1).

Development time on oak (young = 22.0 days, CIs: 18.6, 25.4; old = 22.3 days, CIs: 18.3, 26.4) was not significantly different from that on sycamore (young = 29.0 days, CIs: 22.3 days, 36.2; old = 25.0, CIs: 18.3, 32.1), but was significantly lower than on birch (young = 27.2 days, CIs: 25.0, 30.0; old = 29.6 days, CIs: 27.4, 31.8)(Figure 5.4). In the sycamore treatments, however, only a single individual fed on each leaf age group survived to pupation. There were no significant differences in development time between young and old foliage on each species (see Appendix 1, Table S5.2).

5.4.2. Cumulative survival across time and growth rate

On young foliage, cumulative probability of survival declined across time on sycamore (slope = -5.68, CIs: -6.71, -4.37) and was not significantly different on oak (1.07, CIs: -0.37, 2.39). However, cumulative probability of survival declined at a slower rate on birch (2.34, CIs: 0.76, 3.84) (Figure 5.5). There was no significant difference between slopes on older or younger foliage across all species (sycamore = -0.73, CIs: -1.91, 0.55; birch = 1.5186, CIs: -0.33, 3.49; oak = 0.49, CIs: -1.26, 2.34). On birch, after an initial steep decline, cumulative survival

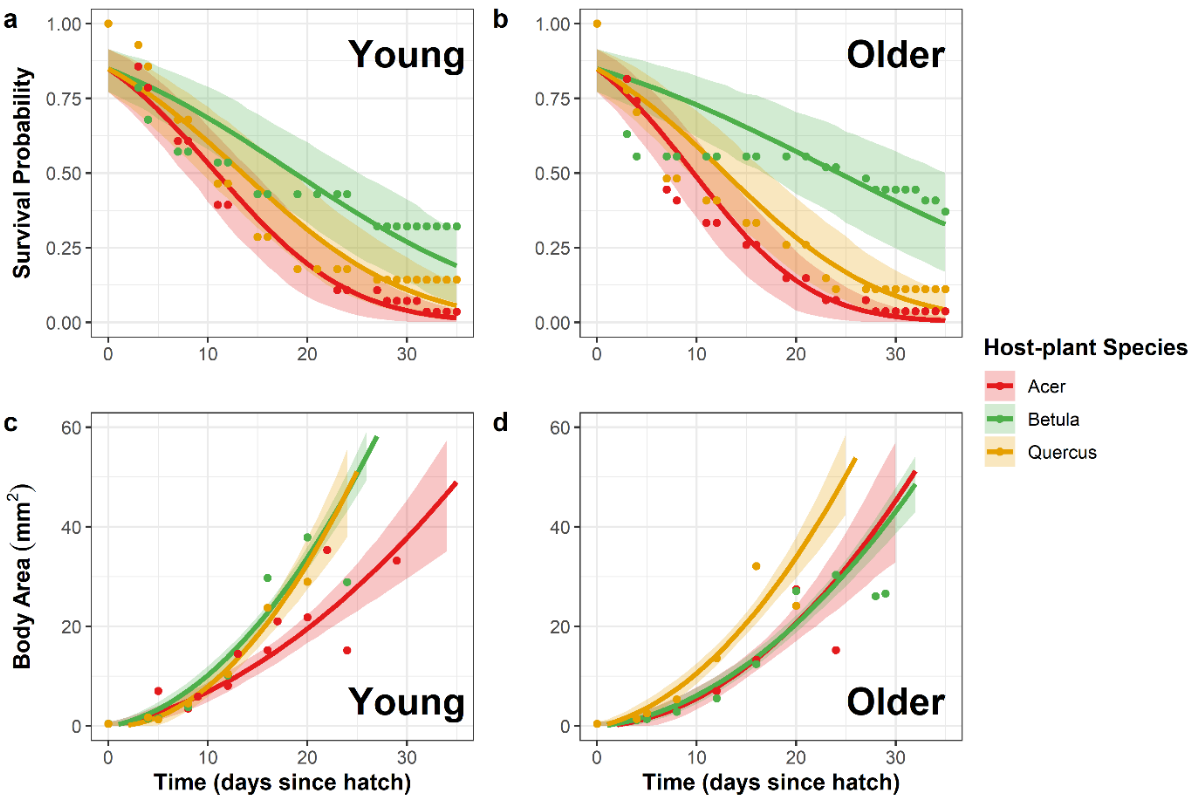


Figure 5.5. Cumulative survival probability (a-b) and growth rate (c-d) across time for caterpillars fed on young and older foliage of three host-plant species (±95% CIs). Points show means of raw data. In c and d predictions are estimated up to the date of the upper bound of the 95% CIs on development time for each treatment group—this was intended to better illustrate the feasible limits of size which caterpillars could attain, and not project beyond the limitations of development time on that host-plant treatment.

probability levels off, considerably (Figure 5.5)—particularly on older foliage. This means that as caterpillars become older it becomes less likely that they will die when feeding on older birch foliage (see also Appendix 1, Table S5.3).

Caterpillar growth increased quadratically on sycamore (day^2 = 0.03, CIs: 0.01, 0.05), but the rate of that quadratic increase was higher on both oak (0.05, CIs: 0.02, 0.09) and birch (0.04, CIs: 0.01, 0.06) (Figure 5.5). On older foliage, however, growth rates on birch were reduced relative to that on younger foliage (-0.04, CIs: -0.09, -0.01). As such, on older oak foliage we see a higher developmental rate than on both other species (Figure 5.5; Appendix 1, Table S5.4).

Estimates of the between brood variance (213.90, CIs: 0.00 736) and between tree variance (98.89, CIs: 0.00, 337.50) in the intercept of the survival slope were substantial, although the lower bound of the credible intervals approached zero in both cases (Figure 5.6). For growth rates, there were similar results (between-brood = 0.47, CIs: 0.00, 1.72; between-tree = 0.16, CIs: 0.00, 0.60) (Figure 5.7). In both cases, however, between-tree differences are around half as influential as between-brood differences (see Appendix 1, Tables 5.3 and 5.4).

5.4.3. Identifying an optimal measure of larval development

Both area (Figure 5.8a; slope = 1.34, SE = 0.09, t = 15.24, p = 0.00, R^2 = 0.60) and length (Figure 5.8b; slope = 4.03, SE = 0.29, t = 13.76, p = 0.00, R^2 = 0.55) were highly associated with caterpillar mass, although by inspection of the data this association becomes less precise with increasing caterpillar size (see Appendix 1, Tables S5.5 and S5.6). Area and length were strongly associated with one another (slope = 0.42, SE = 0.01, t = 71.26, p = 0.00, R^2 = 0.91) and this increased, although not by large amount, when the model included a quadratic effect of area (slope = 0.74, SE = 0.01, t = 65.87, p = 0.00, R^2 = 0.97) (Figure 5.8c; see also Appendix 1, Tables S5.7 and S5.8). Ultimately, area was selected as the optimal measure of larval development for the analyses here because it was slightly more closely associated with caterpillar mass, which is an important metric of development with major implications in later life history stages and eventual fecundity and fitness (see Appendix 2).

5.5. Discussion

5.5.1. Effects of early host-plant maturation on fitness

I found no significant differences in either mean probability of survival to pupation or development time between young and older foliage within each host-plant species (Figure 5.4). In almost all cases, the rate at which cumulative probability of survival declined did not differ between young and old foliage. In the literature it is frequently stated that winter moth caterpillars undergo their highest mortality in the earliest stages of their growth, while in the first few instars (Varley *et al.*, 1974; Zalucki *et al.*, 2003; Despland, 2017). Here I find that, while there is certainly a steep decline in survival probability, it is fairly constant, in most cases, throughout development (though see birch, Figure 5.5). Growth rate too did not differ in most cases between young and old foliage. The young and old foliage on which the caterpillars were reared was collected from two fixed time points in the field and frozen, two weeks apart. As such, the general lack of any negative effect of leaf age on performance suggests that leaf maturation between these two time points (in this particular year) had no

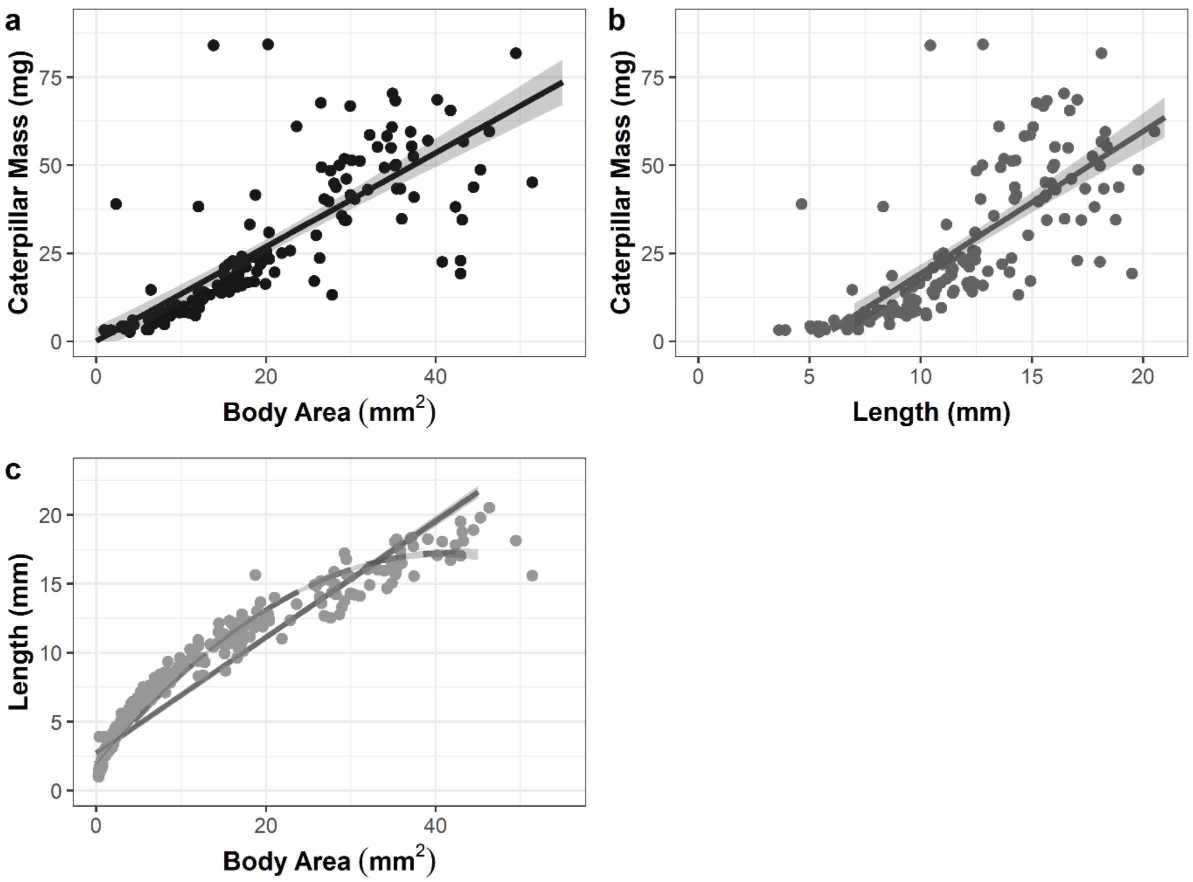


Figure 5.8. Correlations between metrics of caterpillar growth. Body area is the surface area visible in a photograph taken immediately above; length is the distance from the rearmost part of the body to the top of the head (see Figure 5.3). Body area (a; R^2 = 0.60) and length (b; R^2 = 0.55) are highly associated with caterpillar mass. Body area and length are strongly correlated with one another (c), with the association fitting a quadratic function (R^2 = 0.91, dashed line) slightly more than a linear function (R^2 = 0.97, solid line).

effect on foliage palatability. The one exception was birch—on this species, growth rate was reduced on older foliage, as was the rate of mortality across time. That is to say, although caterpillars were increasing in size at a lower rate, they were also dying at a reduced rate, particularly in the latter stages of development (see Figure 5.5). In contrast, on both oak and sycamore, growth rates remain consistent between young and old foliage treatments. This seems to occur in spite of the anti-herbivory defences which rapidly accumulate, particularly in oak, such as leaf toughening, reduced moisture content, and an accumulation of chemicals such as tannins (Feeny, 1968, 1970; Tikkanen and Julkunen-Tiitto, 2003), and seems to support Feeny's (1970) inference that a sudden switch in host-plant palatability occurs later in the process of leaf maturation. While it is possible that the process of freezing leaves may have altered their structure and biochemistry, producing misleading results in both Feeny’s

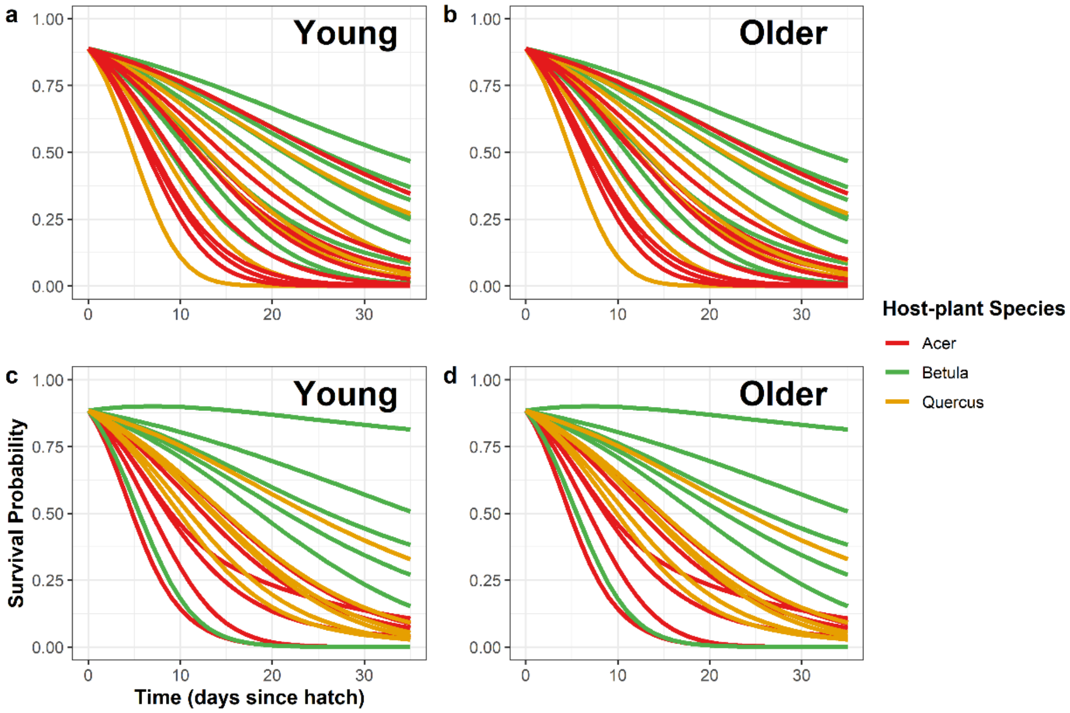


Figure 5.6. Mean estimates of cumulative survival probability for individual host-plant trees (a-b) and different broods (c-d) on young and old foliage of three host-plant species. In (a) and (b) each line represents an individual host-plant tree, in (c) and (d) estimates are shown for each brood on each host-plant species.

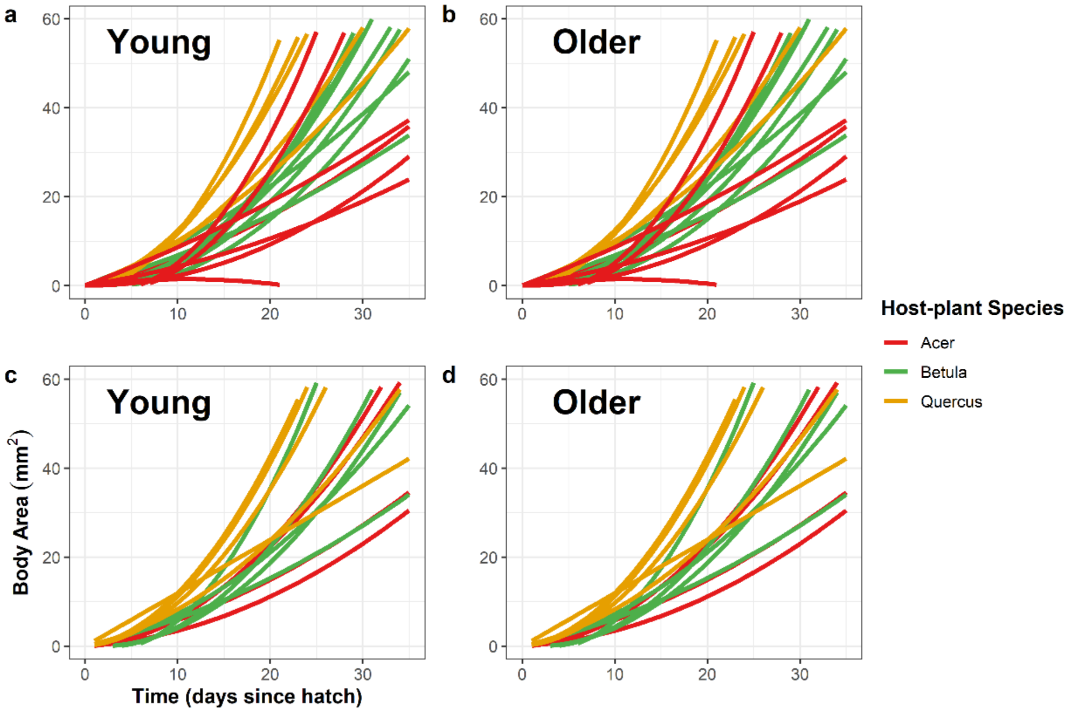


Figure 5.7. Mean estimates of caterpillar growth across time for individual host-plant trees (a-b) and different broods (c-d) on young and old foliage of three host-plant species. In (a) and (b) each line represents an individual host-plant tree, in (c) and (d) estimates are shown for each brood on each host-plant species.

experiments and my own, I found that many of the performance metrics measured here (e.g. mean survival) produce values largely in agreement with those I obtained in Chapters 2 and 3, where caterpillars were fed fresh, unfrozen foliage. This indicates that the freezing process may not greatly alter palatability in these host-plant species.

5.5.2. Poor quality host-plants and a "race to pupation"

Overall mean levels of survival were highest on birch and the cumulative survival across time was consistently higher on this species, which contrasts with the widely held view that oak is the "main" or "primary" host-plant of this species in the field (Table 2.1). Although some literature does indeed find caterpillar performance at its highest on oak out of a range of alternative hosts (Vanbergen *et al.*, 2003; O'Donnell *et al.*, 2019), the results I present both here and in Chapters 2 and 3, largely accord with one another, despite quite different experimental procedures being used, suggesting they are fairly robust (see Figures 2.3, 3.5, 3.8, 3.7, 5.4, 5.5). In this experiment, although growth rate was found to be consistently higher on oak than in other treatments (except young birch foliage; Figure 5.5), development time on oak was also significantly lower (Figure 5.4). Caterpillars feeding on oak increased in size at a greater rate but also pupated around five days earlier, such that size and mass at pupation—proxies of female fecundity—were in fact likely to simply equal those attained on other host-plants, or perhaps even be lower.

Rapid development under stressful conditions seems to indicate a kind of "race to pupation", where caterpillars attempt to reach a minimum necessary pupation size as swiftly as possible and escape the unfavourable environment. There is some uncertainty as to whether stressful conditions ought to result in accelerated development or not (see Goulson and Cory, 1995; York and Oberhauser, 2002; *versus* Kukal and Dawson, 1989; Awmack and Leather, 2002; Moreau et al., 2006; Bawin et al., 2016). However, in Chapters 2 and 3, I have shown that on oak caterpillar performance is generally quite low, which does suggest that the increased rate of development and growth rate shown here is due to stress. I have found, for example, that the mass of pupae produced from caterpillars feeding on oak is lower than most other plant species (see Chapters 2 and 3). In this experiment, counter-intuitively, I found higher rates of cumulative mortality on younger birch foliage than on older foliage (Figure 5.5.) and, if we accept this as a signifier of stress experienced by the caterpillars on that younger foliage, the increased growth rates would be consistent with the “race to pupation” concept. This behaviour could be triggered by caterpillars recognising that they are feeding on a sub-optimal host (whether due to host-plant species, or changing foliage properties as the plant matures), and could amount to cutting their losses, pupating as soon as developmentally feasible, avoiding further risk of mortality to due foliage properties. Such a mechanism may have the added benefit of reducing exposure to external risks to survival, such as predation and adverse weather conditions. The complex and potentially compensatory interactions that exist between these different variables emphasise the need to avoid focusing on a single attribute of performance and recall the wider ecological context within which a species exists.

Other ecological and environmental factors may influence growth rates on certain plant species, besides the inherent palatability of their tissues. Oak, for example, is unusually rich in the number of insect herbivore species it supports (Southwood, 1961; Kennedy and Southwood, 1984), and so the pressures of inter-specific competition may constrain the time caterpillars can spend feeding on this host. Insectivorous woodland bird species can show clear preferences in foraging habitats, to the level of tree species (Gibb, 1954; Partridge, 1974; Holmes and Robinson, 1981; Werner and Sherry, 1987) and the same may be true of parasitoid species (Ohsaki and Sato, 1994; Rutledge and Wiedenmann, 1999)—this could exert habitat-specific predation pressures on these caterpillars. These factors could combine to make developing more quickly, but to a smaller size, an optimal phenotype on any particular host-plant species. In all cases, these mechanisms would require winter moth caterpillars being able to recognise the host-plant species on which they find themselves, and for that host-plant species to trigger developmental and physiological changes. This is certainly possible—host-plant species, or even different constituent parts of the same host-plant, can induce quite distinct plastic phenotypic responses, e.g. in the case of polyphenism (Greene, 1996, 1999; Noor *et al.*, 2008). Factors such as these must be involved because it is clear that, extrapolating from Figure 5.5, if caterpillars on even older oak foliage continued to feed for only several more days, their increased growth rate would mean a final mass easily in excess of that of caterpillars still feeding on birch and sycamore.

5.5.3. Quantifying caterpillar development

I find that both caterpillar length and dorsal area are effective methods of quantifying caterpillar growth, and are strongly associated with mass (a good predictor of future fecundity, see Appendix 2). However, the degree of this association seems to decrease as caterpillars grow to larger sizes. Many studies attempt to measure caterpillar mass directly to quantify size or growth (e.g. Naef-Daenzer and Keller, 1999; Tikkanen et al., 2000; Schöll *et al*., 2016; Macphie *et al*., 2020; Nadolski *et al*., 2021), which is useful but practically difficult in early instars because of the small size of individuals. This may be of considerable consequence if growth and survival during these stages is of particular importance (Varley *et al.*, 1974). For lab studies at least, length and area represent viable and accurate alternative methods for quantifying growth. Both metrics are suitable means of quantifying growth, and are highly correlated with one another, though area is slightly more predictive of mass but is more time consuming to measure. Since the method I employed here involved photographing individual caterpillars and extracting data later using image analysis software, rather than directly measuring each individual, this method could also reduce handling time for both wild caught or captive reared insects. Calculating length and width to estimate volume would be another potential approach (e.g. Shutt *et al.*, 2019) but I consider this to have several potential drawbacks. Area, viewed directly from above, can be thought of as a cross-section through the widest part of the caterpillar and, since it is directly measured, is more accurate and can account for the flexibility of the caterpillar cuticle (see Figure 5.3). Volume, estimated from the length and width of the caterpillar, will not be able to take account of this variation in body shape as adequately.

5.5.4. Population-level buffering against phenological variability

In an uncertain environment, organisms can adopt a diversified bet-hedging strategy, producing a range of different phenotypes among their offspring, which increases variance in survival within a brood but reduces the long-term variation in mean geometric fitness (Dempster, 1955; Cohen, 1966; see also Chapter 6). Equally, variable environmental conditions can promote phenotypic variation in organisms (Schindler *et al.*, 2015). High levels of environmental variation, therefore, could act to buffer caterpillars, at the population level, against uncertainty in their environment and, by extension, future changes to that environment. Here, I found substantial variation in the intercept of the slope of both cumulative survival across time and growth rate among broods and individual trees (see Section 5.4.2; Figures 5.6 and 5.7). Caterpillars were fed on foliage from the same individual tree throughout their entire development, as would be the case in nature. This suggests that among the offspring of a single female moth there is considerable variation in performance in any given treatment environment, and that individual trees of the same species can vary substantially in their palatability to caterpillars at a given point in time.

At least in these data, host-plant species is likely a more important factor in determining caterpillar performance than leaf age, but even within a species there is still considerable among-brood and among-tree variation (Figures 5.6 and 5.7). For example, estimates of mean survival probability on young sycamore foliage ranges from 60% to near 0% between different individual host trees at day 20, and from 25% to 0% between broods (Figure 5.6). These estimates are likely to be poorly resolved, due to small sample sizes, but do serve to illustrate, even approximately, the extent of the variance that exists. If this variation has an additive genetic basis, such high levels of variation could be maintained in the population due to the heterogeneous nature of the tree species comprising a woodland environment, and the seeming inability of flightless female winter moths (Skinner, 2009; Waring *et al.*, 2017) to discriminate between host-plants (though see Connell, 2013). We may expect to see this kind of variation in fitness depending on host-plant species particularly where there are strong antagonistic pleiotropic effects on differential fitness across host-plant species. Such trade-offs in performance between host-plant species are generally assumed to operate on insect herbivores (Joshi and Thompson, 1995; though see Futuyma and Philippi, 1987). Recalling the cross-sectional way in which the host-plant population was sampled across different dates in this experiment, differences in performance between different individual trees could be accounted for either by intrinsic differences in the baseline palatability of different trees, or differences due to each tree being at a slightly different stage of bud-burst and leaf maturation. Although most trees were at a qualitatively similar stage of development (Bud Stage 3, see Chapter 4), and leaf collection was commenced when leaves were on average at bud-burst across all three species, samples were intended to encompass slight individual variation in phenological stage evident in the field.

On the one hand, high levels of variation in performance (in a given situation) among the offspring of a single brood serves to buffer an individual female against the uncertainty of the environment which their progeny will find themselves in. On the other hand, between-tree differences in the rate of phenological development at the beginning of spring buffers the caterpillars, at the population level, against mismatch with any one tree individual, or species. A spring woodland is a highly heterogeneous environment, a patchwork of different host-plant species at different stages of phenological development, with changing fitness implications. For a hatching caterpillar, therefore, its environment is a mosaic of potential trophic match and mismatch. While at the local level individuals may find themselves mismatched with a food supply, or on a sub-optimal host-plant species, in aggregate across the population, variation in both the phenological stage of different trees throughout a particular site, and high levels of within-brood variation in caterpillar performance on different host-plant species, mean that on average at the population level caterpillars are buffered against uncertainty in their conditions.

5.5.5. Conclusions

I found that the effects of leaf maturation over a two week period after bud-burst on winter moth caterpillar performance were limited, across all host-plant species analysed. This is consistent with Feeny's (1970) suggestion that leaf maturation taking place later in the development of caterpillars may be responsible for driving selection for synchrony in this species. By contrast, host-plant species is an important factor in determining caterpillar performance. Growth rates and cumulative survival varied among species and, in some cases, foliage of different ages on the same species. Contrary to the widespread assumption made by much of the literature, oak was found to be a sub-optimal host, with low survival levels, rapid development time, and increased growth rate (which may be indicative of stress). In addition, considerable variance was found in caterpillar performance among broods and among the foliage of different individual trees. This variation may contribute toward acting as a buffer for individual fitness and caterpillar populations against trophic mismatch at a local level, and could perhaps ameliorate the impacts of increased mismatch brought about by climate warming.

The Patchy Onset of Spring

A deciduous woodland at Culross, Fife (United Kingdom), 2022

Chapter 6: ‘Buffering’ and stability under changing environmental conditions

“Individuals die, populations disappear, and species become extinct. That is one view of the world. But another view of the world concentrates not so much on presence or absence as upon the numbers of organisms and the degree of constancy of their numbers.”

—C. S. Holling, 1973

6.1. Abstract

Organisms and their populations are often remarkably persistent in natural environments, even in spite of change, uncertainty, and unpredictability in the biotic and abiotic conditions which they experience. With the climate expected to continue warming, most work tends to focus on the deleterious consequences for natural populations and fails to adequately consider the extent to which organisms may be able to endure these changed conditions and their populations remain stable. However, this concept of ‘stability’ in ecology is somewhat nebulous. We can describe stability in living systems in a number of ways: remaining unchanged (resistance); returning to a baseline state after a short perturbation (resilience); and persisting over time in spite of such changes (persistence). In the literature on climate change and phenology, we also find the term ‘buffering’ being frequently used, though it has not been systematically defined. In biological systems, I argue that this term usefully encapsulates a propensity towards one or more of these stability concepts and that it (and notions of stability) can be applied across organisational levels in an ecosystem. Individual organisms, populations, communities, etc. that are resistant, resilient, or persistent in the face of an environmental change or environmental variation, may be said to be *buffered* against those changing conditions. I formally define buffering in living systems as *the amelioration of any fitness effects resulting from an environmental change* (see p140). This is achieved through a diverse array of *buffering mechanisms*, including adaptations, phenotypic plasticity, portfolio effects, and bet-hedging strategies. Crucially, where buffering exists as a means of occupying a variable or uncertain niche, those same buffering mechanisms may

impart some stability in the face of the future changes we expect as a result of climate warming. Here, as a case study, I consider phenological mismatch in spring-feeding caterpillars—a widely used model system. I explore ways in which these species, contrary to the popular framing of their ecology, are buffered against the inherent variability and unpredictability of their temporal niche, providing examples to illustrate the presence of potential buffering mechanisms. I discuss how these mechanisms may enhance the stability of populations of these species against changes expected in light of climate change.

6.2. Introduction

Natural environments are seldom, if at all, completely invariant. Organisms find themselves experiencing constant environmental changes of different magnitudes, directions, and frequencies, across a range of spatial and temporal scales. Understanding how genes, individuals, populations, and species respond to environmental change is at the heart of evolutionary biology. Picking apart the effects of such changes on the complex web of biotic intra- and interspecific interactions which make up an ecosystem is a more daunting challenge. There are, in essence, two prisms through which we can view the impact of changing environmental conditions on organisms, their populations, and their communities: one is to focus on the detrimental impacts, on reductions in fitness caused by novel circumstances, on the individuals and populations which are driven to decline and even extinction; the other is to consider the remarkable stability of living systems, from individuals up to the level of entire ecosystems, in the face of often substantial environmental perturbation (Holling, 1973).

The climate, for example, has undergone great changes, even within the recent past (e.g. Kirschvink, 1992; Royer *et al.*, 2004; Kasting and Ono, 2006; Doney and Schimel, 2007; McInerney and Wing, 2011; Lyons et al., 2014; Scotese *et al.*, 2021). Across many millions of years, while some species have gone extinct (Taylor, 2004), others have continued unchanged in their external phenotype—a classic example of this is morphological stasis in *Amalda* snails (e.g. Michaux, 1989; Gemmell *et al.*, 2020; reviewed in Gould, 2002). Recognisable ecosystems and biomes can persist, despite turnover in their component parts (Stenseth and Smith, 1984). Even at a very small spatial scale, we see temporal variation in the conditions with which organisms must cope—in temperature, solar radiation, precipitation, food availability, etc. To give two concrete instances: at Dawson City, in the Canadian territory of Yukon, temperatures across the year range from -30.1°C in January to 23.1°C in July (Canadian Climate Normals 1981-2010, 2022); at an even finer temporal scale, within a single day, temperatures in the Earth's deserts can range from 38°C to -3.9°C (NASA Earth Observatory, 2022). Perhaps the most startling fact is that organisms survive at all, and not that some succumb to the pressures of these conditions and to their living competitors.

These two facts—on the one hand, the variation and often unpredictability of the environmental conditions experienced by species; on the other, the surprising stability of many natural populations and ecosystems, and the ability of organisms to cope with fluctuations in their environment—are particularly relevant in light of modern concerns around the impact of climate warming. Increasing global temperatures are predicted to bring about significant changes to many environments (IPCC, 2021), and the degree to which organisms can absorb and tolerate these changes will be of crucial importance (IPCC, 2022). Whilst much work on the impacts of climate change on populations and communities focuses on deleterious consequences, those mechanisms which have buffered organisms against historical variation and unpredictability in their environment could also act to ameliorate the effects of future extrinsic changes, such as those threatened by climate change. That is to say, species used to coping with change or uncertainty in particular aspects of their environment may be better able to cope with those conditions changing in future. The term 'buffering' is one widely used in a general sense in the literature to allude to this sort of effect (e.g. Roland and Myers, 1987; Burgess *et al*., 2018; Wang *et al*., 2020; de Villemereuil *et al*., 2020; De Frenne *et al*., 2021), but little effort has been made systematically explore this idea.

A classic and widely discussed example of climate change potentially causing significant disruption to a natural community is as a driver of phenological mismatch in the tree/caterpillar/bird food-chain, ubiquitous in temperate spring-time woodland environments (Visser *et al.*, 1998; Tikkanen and Julkunen-Tiitto, 2003; van Asch and Visser, 2007; van Asch *et al.*, 2007, 2012; Charmantier *et al.*, 2008; Both *et al.*, 2009; Both, 2010; Burgess *et al.*, 2018; Samplonius *et al.*, 2020). Typically, the literature emphasises the negative impacts of climate warming on this system—that it will lead to the disruption and mistiming of previously temporally synchronised trophic interactions. Species at each of these trophic levels, however, possess attributes which likely act to reduce the negative impacts of any mistiming—which 'buffer' them against it. Here, I examine the concept of buffering in detail and use the tree/caterpillar trophic interaction as a case study in which to explore how it might operate in nature. I will survey concepts of ecosystem stability, how we can apply these across structural levels within an ecosystem, and how these relate to the idea of buffering. I will explore how the mechanisms which allow spring-feeding caterpillars to cope with the inherent variability and unpredictability of their niche may be reimagined as safety-nets against climate change, acting to ameliorate some of the negative impacts of these long-term changes in the same manner.

6.3. Concepts of stability in living systems

In terms of modelling and making theoretical predictions which relate to the stability of living systems, there has been a great focus on simple quantitative models growing out of the physical sciences (Holling, 1973) but individual organisms, let alone entire ecosystems, are so complex that they cannot be completely described in this way (Hall and Deangelis, 1985). They are expansive, multidimensional systems, often with countless component parts, and our conception of what stability means for such a system must necessarily depend on our frame of reference—on the way we choose to delimit this complexity. That the complexity of ecological systems is an obstacle to clearly defining ‘stability’ is evident when we consider the abundance of definitions which have been proposed: Grimm and Wissel (1997) conducted a systematic review of the literature, and found 163 definitions of stability relating to ecosystems, using 70 different stability concepts and 40 different measures of stability. As well as suggesting an inherent difficulty in precisely pinning down the concept and a general vagueness in its application, this abundance of terminology also hints at a deep interest among biologists with the idea of ecological stability. Here, I treat the word in its vernacular sense, and use it only as an umbrella term, encompassing all the more precise definitions I outline below.

The importance of clearly describing our frame of reference before attempting to define stability is easy to illustrate: the survival probability of individuals could decline, but fecundity could increase; a population could remain constant in abundance, while declining in biomass; the species richness of a community could remain the same but the relative abundance of its constituent species could become less even. The extent to which the properties of many natural systems—both living things and aspects of their environment—can appear to vary often depends on the scale at which these properties are considered: what can seem highly heterogeneous at a fine-grained scale can appear relatively homogenous at a coarser scale (Levin, 1992). In order to properly conceptualise stability, therefore, the frame of reference of our definition must be carefully delimited in a number of respects (Grimm and Wissel, 1997):

(1) The level of organisation to which it is applicable (individual, population, species, etc.)

(2) The variable quantifying stability (abundance, biomass, biodiversity, etc.)

(3) The reference, baseline conditions against which comparisons are being made (these may be static, such as a mean fitness value or mean abundance; or dynamic, such as regular, cyclical trends across space or time)

(4) The nature of the disturbance (in terms of magnitude, frequency, duration, etc.)

(5) The spatial and temporal scale at which the concept applies

From this, we can then consider an appropriate definition of 'stability'. Grimm and Wissel (1997) distilled three fundamental meanings of the term 'stability' in the ecological literature: "(1) staying essentially unchanged, (2) returning to the reference state (or dynamic) after a temporary disturbance, and (3) persistence through time of an ecological system" (p326). *Constancy* describes a system remaining largely unchanged, and *resistance* describes constancy in the face of a disturbance, or environmental change (Figure 6.1). Systems perturbed by environmental changes but which return to an equilibrium, pre-existing state are said to be *resilient*, and the speed with which they return to that state is a measure of their *elasticity* (the "engineering resilience" of Holling, 1973) (Figure 6.1). Biological systems which are maintained through time are said to be *persistent*. Unfortunately, many of these terms still find themselves being employed with quite different meanings, highlighting the importance of clearly defining any terminology used. These concepts can largely be applied across the organisational levels within an ecosystem, although in each case the metrics through which it makes sense to interpret stability will vary. Indeed, as emphasised above, the assessed stability of a system can vary based on the level, metric, and temporal or spatial scale chosen.

6.4. 'Buffering' and stability

Stability and buffering are related, in that they describe different aspects of the same phenomenon. Biological systems which are stable—whether resistant, resilient, or persistent— under changing conditions may be said to be *buffered* against those changes (Figure 6.1). Stability under changing conditions is determined with respect to a historical

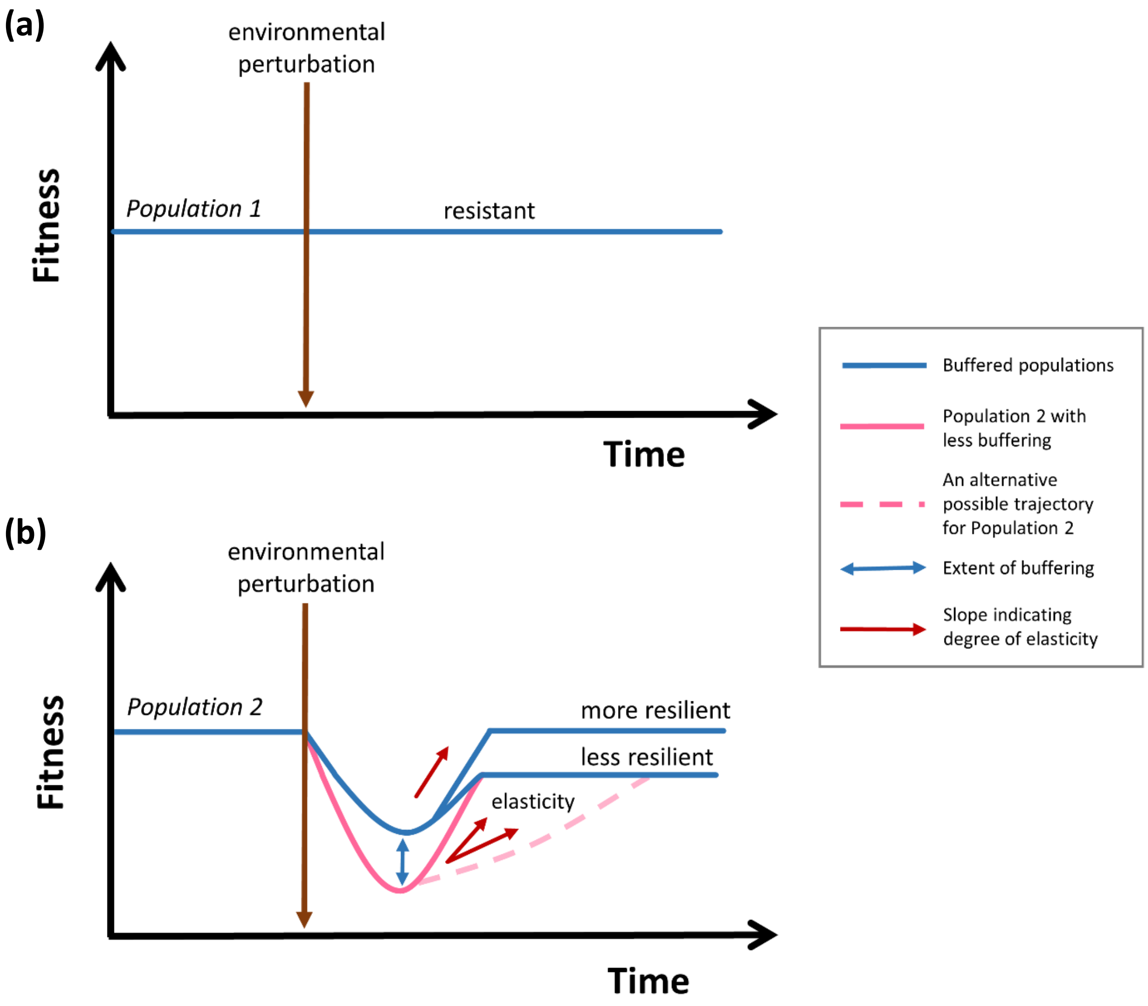


Figure 6.1. Schematic illustrating the conceptual differences between buffering and various forms of stability. Two populations move through time and are subject to an environmental perturbation. The diagram shows "fitness", but this axis could equally well represent other metrics, such as biomass, population size, etc. In (a) Population 1, the fitness of that population remains constant in spite of the disturbance: this population is therefore said to be *resistant* to the change, in terms of its fitness. (b) Population 2 shows a brief decrease in its fitness following the perturbation, which then rebounds: this population is said to be *resilient*. Both populations are *buffered* against the change. If they were not buffered, the environmental disturbance would cause a greater change in their fitness. This is illustrated in Population 2, where the pink line shows the fitness change over time of the population had it not been buffered, or had it been buffered to a lesser extent. Without buffering, Population 2 is still resilient, but suffers a greater perturbation in fitness. The *elasticity* of Population 2 under various scenarios is indicated by the gradient of the red arrows—this shows the speed with which it returns to its prior state. The alternative trajectory for Population 2, indicated by pink dashed lines, shows how a population may be equally resilient, but less elastic in changed or disturbed conditions. Resilience does not necessarily imply that a population will perfectly return to its previous fitness state, and in (b) two different possible levels of resilience are illustrated. In one case, the population returns to a lower fitness than before ("less resilient"), and in the other the previous level of fitness is restored ("more resilient"). This serves to distinguish *degree of resilience* and *buffering*, which are distinct phenomena.

baseline, while buffering rather describes the fact that the effect of a potential disturbance or environmental change has been reduced or dampened. For example, burrowing desert animals may be said to be buffered against high daytime temperatures by seeking refuge underground (Costa, 1995). Certainly, this implies individuals are resistant to and can persist in spite of inhospitable conditions, but our use of "buffering" suggests something subtly different—that this behavioural mechanism is dampening out the effects of the high temperatures. I therefore define buffering as *the amelioration of any fitness effects resulting from an environmental change* (Figure 6.2). The mechanisms which contribute to the stability of living systems under changed conditions can be thought of as *buffers* or *buffering mechanisms*. Stability in the face of changing conditions is therefore at least partly a result of buffering, and the operation of buffering mechanisms in individuals, species, populations, etc.

Buffering can arise as a means of coping with variation, uncertainty, or unpredictability inherent in some aspect of the environment but, particularly across organisational levels (Figure 6.3), it is not necessarily adaptive. Ecosystems may be buffered against environmental change due to an inherent property of the system that has not been evolved and directly selected for at the ecosystem level (such as portfolio effects; see Section 6.6.4). This contrasts with, for example, behavioural buffering mechanisms at the organism level, which have arisen as a direct result of selection and are adaptive. However, all buffering mechanisms which act

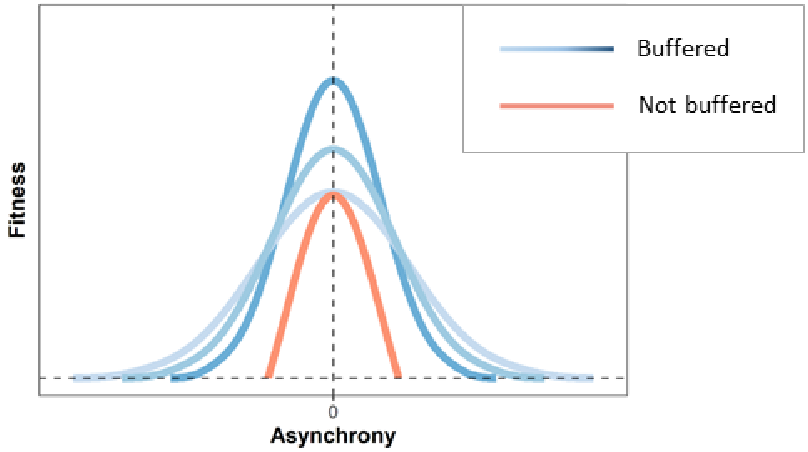


Figure 6.2. The hypothetical effects of buffering on fitness, illustrated by the match-mismatch hypothesis (see Section 6.5). Fitness (e.g. the mean geometric fitness of a population) declines steeply with increasing asynchrony in the absence of buffering (pink). Where populations are buffered to varying degrees (shades of blue) the fitness effects of asynchrony are ameliorated, so that fitness is higher than it would have been for any given amount of asynchrony, relative to an un-buffered population.

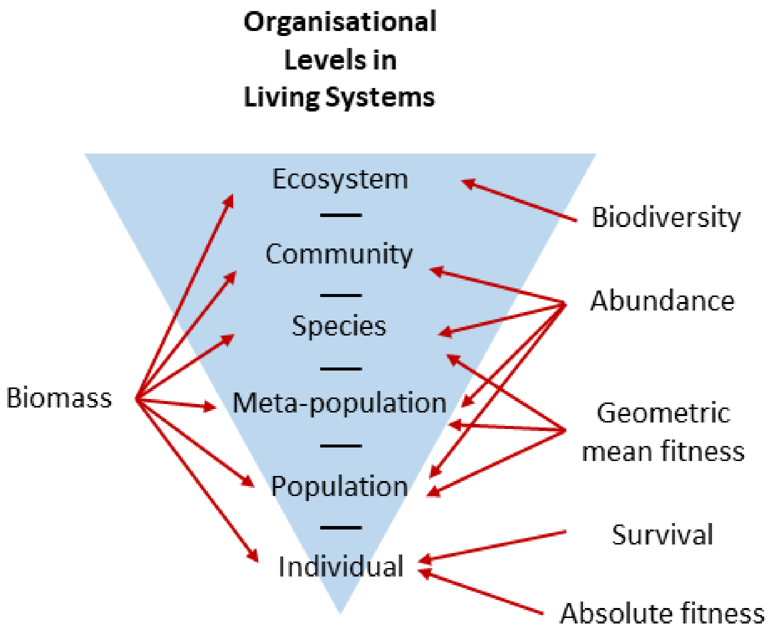


Figure 6.3. Organisation levels across which buffering could act, and a selection of metrics to quantify it. The particular metrics chosen will depend on what is of interest in any given situation. Whether or not buffering is occurring will depend on the organisation level and the metric chosen to quantify it. Different combinations of these may yield different results, e.g. the size of a population may be buffered but the mean geometric fitness may not.

to maintain stability within the spectrum of changing environmental conditions likely to be experienced historically might also, by extension, impart stability in the face of novel, extrinsic environmental changes. Populations resistant to within- or between-year climatic variation at a local scale, for example, might find themselves well placed to persist when subject to global climate change. Such populations could be said to be buffered against temperature variation and also potentially buffered against climate change.

There is an inherent danger in ascribing a precise, technical, discipline-specific definition to any word which is common parlance. However carefully defined, the technical and vernacular definitions of that word tend to compete within the literature, leading to confusion. In this case, however, I think this act is justified and holds less danger. Buffering is a concept or principle, and it is much less important what we call it than that we appreciate its distinction. Further, we can frequently find buffering used in the literature in a sense broadly in agreement with the formal definition I have outlined, such is the concordance between the definition I have offered here and the common, descriptive definition (some examples include: Burgess *et al.*, 2018; Wang *et al.*, 2020; de Villemereuil *et al.*, 2020; Ma *et al.*, 2021;

though for a use of ‘buffer’ in a subtly different or more colloquial sense see, for example: Roland and Myers, 1987; Yachi and Loreau, 1999; Olliff-Yang *et al.*, 2020; Iler *et al.*, 2021). My purpose here, then, is less to add another term to a literature already replete with them, but more so to draw attention to and clarify this potentially significant concept. The definition I have offered here is also strictly a biological one—buffering is described as a property of living things. De Frenne *et al.* (2021) offer a formal definition of buffering in relation to microclimatic *environmental conditions*, specifically as a dampening of temperature fluctuations. Although focused on the environment more than organisms and living systems themselves, this reflects closely the definition I have given here.

6.5. Buffering and the match-mismatch hypothesis

Climate warming is causing widespread changes in the phenology of animals and plants—in spring, temperature increases are causing a general advancement of phenology, across a range of taxa (see Chapter 1). For species which rely on timing a stage in their life history with that of another species, widespread phenological changes are potentially very deleterious. If two interacting species, such as a consumer and its resource, respond to this increase in temperature by advancing their phenology to different degrees then they may become mistimed relative to one another, or *asynchronous*. If the consumer suffers negative fitness consequences as a result of phenological asynchrony, it is said to be ‘mismatched’. This idea has become formalised as the match-mismatch hypothesis (MMH), and has been the subject of a great deal of interest among ecologists in recent years (see Chapter 1 and Appendix 4). There is concern that climate change, driving various phenological changes, could disrupt synchrony between many different species, across animal and plant communities, affecting, for example, trophic interactions and mutualisms, such as pollinator interactions. This could cause widespread phenological mismatch and reductions in fitness, leading to population declines, perhaps even undermining the integrity and stability of entire ecosystems (Chapter 1 and Appendix 4).

The operation of the MMH depends on two factors: the existence of an ephemeral resource; and, that fitness, recruitment, or some such measure of the performance of the consumer depends in large part on the availability of that resource. For the consumer taxon, all else being equal, these criteria give rise to selection acting to increase the degree of synchrony between the consumer timing and the timing of resource availability. However, where the selective consequences of mismatch are severe, and the ability of the consumer to accurately predict the phenology of their resource is limited or imperfect, the persistence of the consumer over time may, at least in part, be maintained by buffering mechanisms, which ameliorate any negative effects of asynchrony. Many phenological traits depend on meteorological and seasonal conditions as cues or target conditions, which can be difficult to accurately forecast. Thus, variation due to unpredictable weather could occur commonly. Hitherto, the focus has largely been placed on the detrimental effects of mistiming, rather than the ways in which organisms in these putatively phenologically synchronised systems can and do persist in the face of inevitable perturbations to synchrony arising out of inherent uncertainty and unpredictability in aspects of their niche. Further, at the level of individuals, an ability to tolerate variation in the degree to which they are synchronous may present a means by which they are buffered against at least some of what would be the negative effects of mismatch.

The classic tree/caterpillar/bird food-chain of temperate woodlands has become a standard study system in work on the MMH (reviewed in Samplonius *et al.*, 2020; see Section 1.3). This tri-trophic system, about which much is already known, offers an interesting test case where we might consider the role of buffering in allowing these organisms (and systems) to persist under variable or shifting environmental conditions. In line with the focus of this thesis on the tree/caterpillar link of this food-chain, I will use the spring-feeding caterpillar guild as an example in which to illustrate various buffering mechanisms which promote stability under different kinds of uncertainty, unpredictability, or variation in environmental conditions, and how these may also potentially act to buffer these organisms (across organisational levels) against some of the detrimental phenological effects of climate change.

6.6. Buffering mechanisms in spring-feeding caterpillars

6.6.1. A simplified view of the system

As spring approaches, buds break on trees, and the young leaves begin to expand and mature. During this period, leaves undergo significant structural and biochemical changes, both of which affect their palatability to the neonate and growing caterpillars which feed on them (see esp. Chapters 3 - 5). The fitness of newly hatched arboreal caterpillars in spring is therefore dependent to a very high degree on the extent to which they can match the time they hatch to the timing of bud-burst on their natal tree (see Chapters 3 and 4; Tikkanen and Julkunen-Tiitto, 2003; van Asch *et al.*, 2007). In the winter moth *Operophtera brumata*—a widely studied spring-feeding caterpillar species—Embree (1965) estimated that the highest levels of mortality occurred in the first larval instar as a result of selective pressures towards synchrony, eliminating some 85% of individuals which successfully eclosed. English oak *Quercus robur* is widely regarded as the primary host-plant of this species (see Table 2.1), and individuals therefore face strong selective pressures to precisely match the phenology of individual oak trees, in a heterogeneous forest environment, in spite of variation in biotic and abiotic conditions. The trees themselves respond plastically to temperature variation (Buse *et al.*, 1999; Karlsen *et al.*, 2007; Both *et al.*, 2009; Cole *et al.*, 2015; Hinks *et al.*, 2015; Burgess *et al.*, 2018), such that the caterpillars must match a moving temporal window. This widely held perspective, through which much of the work on this system is viewed, is, however, narrow and fails to consider the many ways in which the winter moth and other spring-feeding caterpillar species appear to be at least somewhat resistant or resilient to asynchrony and environmental variation (see Chapters 2 – 4). This provides a useful set of concrete examples to illustrate a range of different buffering mechanisms, operating at a number of scales, organisational levels, and metrics:

- adaptive and plastic mechanisms operating at the individual level to reduce the impacts of mismatch;
- biological bet-hedging, in which unpredictability promotes bet-spreading among offspring phenotypes;
- portfolio effects, where environmental variation promotes phenotypic variation in a population, lessening the impact of those variable conditions at the population level.

I will now consider each of these in turn.

6.6.2. Adaptations and plastic buffering mechanisms

There is necessarily some overlap between these categories, because behavioural, morphological and physiological plasticity can themselves be adaptive. Phenotypic plasticity can act to ameliorate the potentially negative effects of variation in the environment by modulating a phenotype to increase fitness under a given set of environmental conditions. Torpor in insects, for example, can allow them to withstand unpredictable periods of inhospitable temperature conditions (Leather *et al.*, 1993). All forms of homeostatic physiological regulation are examples of adaptive plastic mechanisms by which stability is maintained within an individual organism, and buffer it against variable external environmental conditions (West-Eberhard, 2008). Starvation tolerance (see Chapter 4) would be an example of an adaptation that is not strictly speaking phenotypic plasticity, but which reduces the impact of variation in environmental conditions, and which can allow individuals to persist through periods of fluctuating food availability (Wint, 1983; Stockhoff, 1991; Reavey, 1992). This is an interesting example because it highlights the significance of the metric we use to assess stability in affecting our conclusions: individuals may tolerate periods of starvation and breed successfully, and as such we might conclude that the *size of a population* suffering starvation was *resistant*. However, if the *physical condition* of individuals is *lower*, stability quantified using another metric, such as the mean individual *biomass*, might *not be resistant* to such environmental extremes. Starvation tolerance would therefore buffer population size to a greater extent than it buffers the biomass of a population. Although adaptation and plasticity have knock-on effects on buffering at higher levels of ecological organisation, they operate at the level of individual organisms.

In spring-feeding caterpillars we see evidence for both adaptive and plastic buffering mechanisms. As I have shown in Chapter 4, many caterpillars can tolerate starvation for several days as a strategy for coping with hatching too early—the extent of this ability varies with caterpillar species and with ecological and environmental factors, such as temperature (see Chapter 4; Patocka, 1972; Wint, 1983). The spring leafing phenology of trees can vary both within and between tree species (Lechowicz, 1984; Crawley and Akhteruzzaman, 1988; Kramer, 1995; Karlsen *et al.*, 2007; Basler and Körner, 2012; Roberts *et al.*, 2015; Cole and Sheldon, 2017; Geng *et al.*, 2020). In the caterpillar of the green oak tortrix, a trophic specialist on oak, starvation tolerance is greater than that of species which are more generalist in their diet, reflecting their increased need to match a narrower, more specific temporal window (Hunter, 1990; Ivashov *et al.*, 2002). I also show in Chapter 4 that the caterpillars of the winter moth can utilise the unopened buds of their host-plants as food in many cases. Although this results in higher levels of mortality—which decreases as buds develop—it enables some individuals to persist in the face of otherwise hostile conditions. In Chapters 3 and 5, I discuss the effects of hatching too late: fitness does indeed decline as caterpillars are forced to feed on older foliage, in line with the simplified expectation in this system, but the degree to which it does so varies across different caterpillar and host-plant species. Many spring-feeding caterpillars are therefore able to tolerate feeding on more mature foliage as a result of mistiming—these buffers reduce the impacts of asynchrony, rather than reduce its extent.

In many instances, though not universally, the adult females of spring-feeding caterpillar species, such as the winter moth, are entirely flightless (Skinner, 2009) which restricts their ability to select individual host-plants. In so far as female winter moths can show any host-plant preferences when they eclose from their pupae on the forest floor, they seem to preferentially target larger trees to ascend and lay their eggs (Connell, 2013). Females lay eggs throughout their host tree, on bark, branches and terminal buds with seemingly little discrimination—they will also lay freely in captivity in entirely unnatural situations. Woodland environments are typically a complex mix of many different plant species, all at different stages of succession, growth, development, and at varying relative abundances. This, combined with the limited ability of the females to choose a particular tree on which to oviposit, mean that winter moth caterpillars must be able to cope with a great deal of uncertainty in the food-plant they will find themselves on when they hatch. Ideally they will be able to exploit whatever is available. In line with this expectation, winter moth caterpillars, as well as those of most spring-feeding caterpillar species, are highly polyphagous, and capable of feeding on a broad range of taxonomically disparate plant species (Porter, 2010; Robinson *et al.*, 2010; Henwood *et al.*, 2020). Although there is clear variation in caterpillar performance across different host-plants (see Chapter 2 and 3; and individual host trees, see Chapter 5), a broad diet allows caterpillars to cope with the great degree of uncertainty in their future host-plant that is an unavoidable consequence of their life history. Where the offspring of a particular female find themselves on the same or a similar tree to that of their mother, individuals can tilt the scales in favour of their offspring through maternal effects.

This form of trans-generational plasticity (Uller, 2008) allows the phenotype of offspring to be adjusted based on the environment of the mother (Kuijper and Hoyle, 2015). In the winter moth, this can allow individuals to fine-tune the phenology of their offspring to better match that of a host-plant individual they are most likely to find themselves on (Dongen *et al.*, 1997; Van Asch *et al.*, 2010).

Although adult female winter moths cannot move far from their pupation site, dispersal still occurs within this and other spring-feeding species, and in some cases seems to act as a buffering mechanism. Neonate or early instar caterpillars finding themselves on a particularly poor host tree (e.g. very low palatability, either before bud-burst or because of advanced maturation of foliage) can disperse to a new location elsewhere on the same tree or on another plant. Although the caterpillars of some species may walk (Johns and Eveleigh, 2013), neonate larvae can ‘balloon’ in an attempt to find a new host (Briggs, 1957; Brown, 1962; Edland, 1971; Holliday, 1977; Hunter, 1993; Van Dongen *et al.*, 1994; Zalucki *et al.*, 2003; Legget *et al.*, 2011; Foster *et al.*, 2013; Johns and Eveleigh, 2013). This behaviour, common to many Lepidoptera, spiders, and mites (Bell *et al.*, 2005), involves spinning a length of silk, which is caught on air currents, carrying the small insect to a new location. As a behavioural mechanism for dispersal, it is a very risky strategy. Probability of dispersal therefore likely depends on the severity of the situation the caterpillar finds itself in, and has been shown to be affected by host-plant species, quality of the food-plant material, and the degree of synchrony with the host-plant (Capinera and Barbosa, 1976; Ramachandran, 1987; Bell *et al.*, 2005; Johns and Eveleigh, 2013). In the winter moth, Holliday (1977) suggested that caterpillar dispersal is a highly significant mechanism, and that individual neonates can balloon successively until they reach a host-plant at exactly the correct stage of development to maximise their fitness. In densely treed, woodland environments this may be an effective strategy, but is less successful in fragment habitats (Van Dongen *et al.*, 1994; Tikkanen and Roininen, 2001; Wesołowski and Rowiński, 2006). Dispersal distance and strategy seems to vary with species: winter moths have been found to travel up to 50m, though estimates of distance, even within a species, can vary greatly (Briggs, 1957; Embree, 1965; Edland, 1971). The mottled umber *E. defoliaria* shows perhaps an even greater tendency to spin silk, especially when disturbed and in the early instars (Author, personal observation). Maternal effects (Rossiter, 1991), such as small eggs resulting from high density feeding in the previous season, or a nutritionally poor food source, could influence a pre-disposition to dispersal under stressful conditions (Leonard, 1970, 1970; though see Diss *et al.*, 1996; Erelli and Elkinton, 2000). Indeed, Hunter and Elkinton (2000) have even suggested that dispersal could reduce the burden of density-dependent mortality due to parasitoids. Caterpillar ballooning does seem to be a major source of dispersal in the wild, though the extent to which it is frequently employed, or is a strategy of last resort, is as yet unclear.

Although synchrony is important for the fitness of individual caterpillars, it matters within fairly broad bounds—individual caterpillars are buffered against asynchrony, on a scale of weeks and months, rather than days (Chapters 3 and 4). Not only can caterpillars tolerate slightly older, mature foliage, and bore into under-developed buds when necessary, they can consume a wide range of host-plant species to allow them to make use of many of the potential plant species they might find themselves on when they hatch. Where palatable food is not yet available caterpillars can withstand periods of starvation, or risk dispersal to a new location. Under changing environmental conditions, these individual-level buffering mechanisms may impart some stability on the size of populations and meta-populations of species in the guild, and the wider communities of which these species are a part.

6.6.3. Biological bet-hedging

Bet-hedging (Slatkin, 1974) is an evolutionary strategy arising from the interaction between mean and temporal variance in fitness. Where there is temporal variation in the fitness of a genotype[4], due to analogous variation in the environment, its long-term success is highly sensitive to occasional very low fitness values (Dempster, 1955). A genotype with lower mean fitness can be favoured over one with higher mean fitness if its fitness has sufficiently low variance (Childs *et al.*, 2010)—if, across generations, one genotype has a low but consistent fitness and another genotype has a generally high fitness with a low probability of fitness being zero, the former may nevertheless be favoured by selection because it only takes one generation of zero fitness to eliminate the latter genotype. In other words, selection favours higher geometric, rather than arithmetic, mean fitness (Dempster, 1955). In the classic example, annual plants, whose seedlings germinate in highly unpredictable, variable

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[4] 'Genotype' is used here in a broad sense to indicate the complete set of genes making up an organism.

conditions, ensure that only a fraction of their seeds germinate in each year (Cohen, 1966). This strategy means they can fail to capitalise on particularly good years, where fitness could be maximised by all seeds germinating, but it allows them to avoid a single catastrophic weather event (such as a sudden drought) killing off all their seedlings, leaving them with no progeny (Cohen, 1966). Essentially, this spreads the risk of mortality across the individual progeny of a single parent. This "diversified" bet-hedging (Philippi and Seger, 1989) involves variation in the phenotype of the offspring of an individual being increased so as to cover a range of different environmental conditions, where the precise environmental conditions expected in future are difficult to predict. This results in an equivalent increase in the variance of offspring survival or individual fitness, but it reduces long-term variation in average fitness across time (i.e. mean geometric fitness). In contrast, "conservative" bet-hedging involves minimising risk at an individual level—variation in fitness among offspring is decreased, but at a cost of also lowering overall mean fitness (Philippi and Seger, 1989). An example of this could be birds producing clutches of a fixed size every year, which may not be optimal in all years but which reduces overall variation in fitness outcomes (Olofsson *et al.*, 2009)—reducing the likelihood of an outcome of zero.

In the timing of caterpillar feeding strategies, we can see both conservative and diversified bet-hedging. Caterpillars feeding late in the season adopt a conservative strategy with respect to host-plant phenology—their fitness is reduced by having to devote resources to overcoming late-season plant defences accumulated as the foliage matures, but they can be certain that foliage will be available for them to feed on. The onset of spring, on the other hand, is difficult to predict, so species wishing to exploit the window of poorly defended, young foliage have to cope with that uncertainty. Polyphagy may arise as an individual-level adaptation and if, as seems likely, fitness is generally traded-off across host-plants (Bernays and Graham, 1988; Schoonhoven *et al.*, 1998; Singer, 2008)—that improving performance on one host-plant species comes at the cost of decreasing fitness on another—then it is also a diversified bet-hedging strategy. Geometric mean fitness is maximised through generally low arithmetic fitness on all host-plant species to avoid a fitness of zero on one particular host-plant species—this would be catastrophic since a female winter moth, for example, will only ever lay on a single host-plant individual (see Figure 1.4).

To help time their hatch to coincide with the flush of foliage in spring, the development of spring-feeding caterpillars follows many of the same climatic cues used by their host-plants to trigger development (Visser and Holleman, 2001; Both *et al.*, 2009; Hibbard and Elkinton, 2015; Marchin *et al.*, 2015; Burgess *et al.*, 2018). Temperature conditions particularly play a key role in driving development rate and hatching (Hibbard and Elkinton, 2015). This overarching plastic buffering mechanism (see Section 6.6.2) allows caterpillars to hatch approximately in accord with the timing of their host-plants. But the development of their host-plant will vary across species, habitats, and even individuals of the same species, and none of these factors can be accurately predicted in advance (Figure 6.4). Within caterpillar broods, however, there is considerable variation in the thermal requirements to stimulate hatching, such that in the winter moth, for example, the timing of egg hatching can range over a month in the field and within broods from a single female (Watt and McFarlane, 1991; Buse and Good, 1996; van Asch *et al.*, 2007). Even under identical environmental conditions, individuals from the same brood can hatch up to several weeks apart (Speyer, 1938; Ivashov *et al.*, 2002; Tikkanen and Julkunen-Tiitto, 2003). Phenotypic diversity in phenology ensures that, in spite of the difficulty in predicting host-plant phenology, at least some of the offspring of any given female moth will hatch at an appropriate time. This diversified bet-hedging strategy buffers broods against the effects of mismatch by spreading the risk among all the individuals in that brood, maximising geometric mean fitness. Related to this example, the fact that females lay slowly over several days may also be an example of a bet-hedging approach—as the insect ascends and moves around the tree it is likely she will oviposit in a range of different thermal environments, and adjacent to different regions of foliage with varying spring phenology (fitness can vary between different parts of the same tree, e.g. Suomela et al., 1995). While bet-hedging approaches are an evolutionary strategy that operates at an individual level (in this case, the parents rather than the offspring), they too can indirectly impact the stability of populations, and higher organisational levels.

6.6.4. Portfolio effects

Diversified bet-hedging, where between-generation variation in average offspring outcome is minimised by a diverse range of offspring phenotypes within-generation, is one example of a portfolio effect. But not all portfolio effects are forms of diversified bet-hedging. ‘Modern

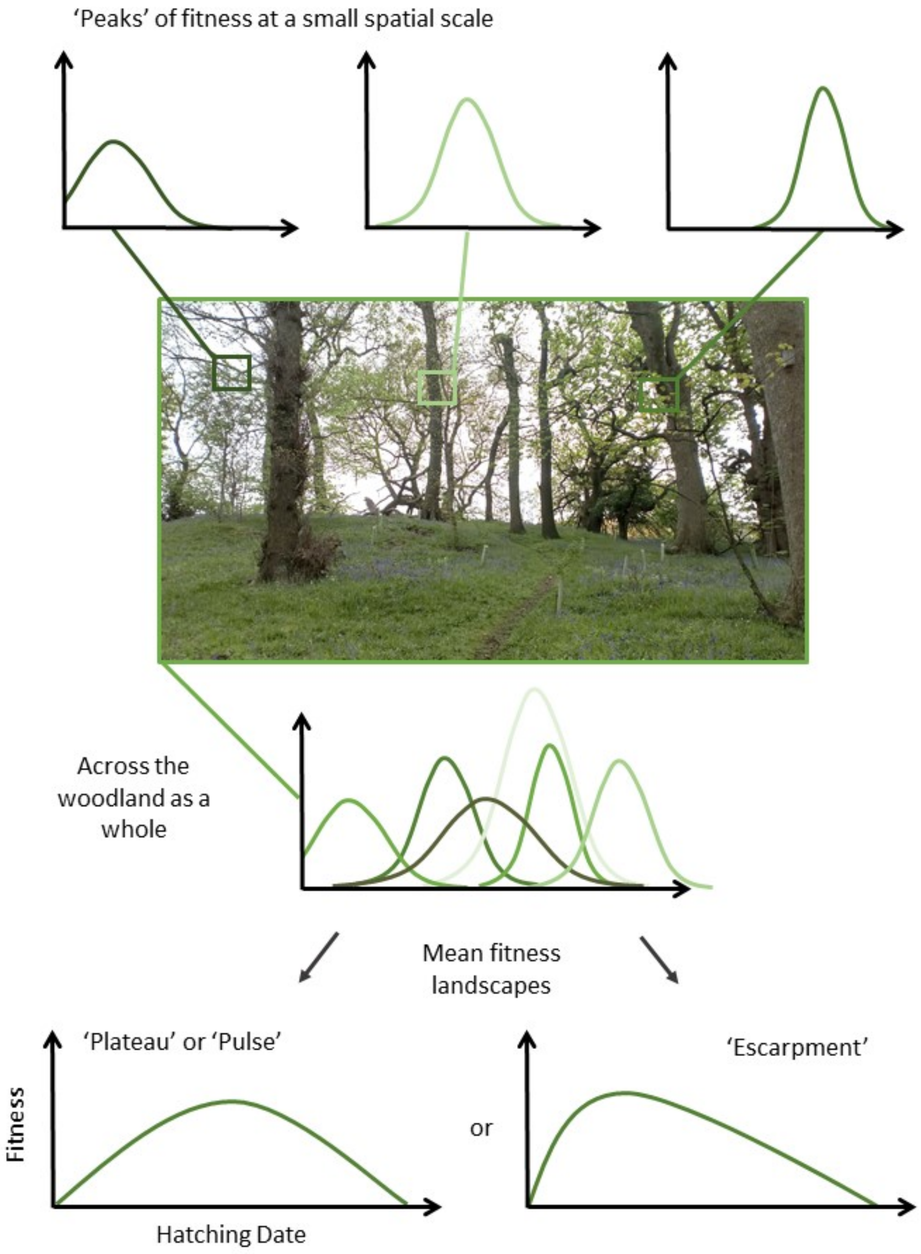

Figure 6.4. Selection for synchrony at a small spatial scale in a variable environment can dampen selection at a larger spatial scale. Assuming that the fitness costs of asynchrony for any individual locally is severe (i.e. the fitness curve is steep), across an entire population these many small and steep peaks may still average out to a broader, flatter, shallower fitness curve. Spatial variation in selection for synchrony of this kind could lead to the evolution of a diversified bet-hedging strategy for caterpillar hatch date, promoting variation in caterpillar phenology. Depending on the extent to which the selection against late and early hatching is symmetrical, the fitness profile may be either a broad, plateau-like pulse, or a skewed escarpment-like shape, rather than a sharp peak.

portfolio theory' is an economic model introduced by Markowitz (1952), which contends that the volatility of an investment portfolio is a function of the correlation between the different components of that portfolio and, as such, diversification can reduce volatility in returns. In essence, increased variation in investments dampens variation in the returns of those investments. In biology and ecology, portfolio effects occur in a much wider range of instances than diversified bet-hedging, which tends to apply at the level of individuals and is an evolutionary strategy adopted by organisms. Portfolio effects can include a range of non-living properties of habitats and environments, and can act across organisational levels.

Portfolio effects can apply to biodiversity in ecosystems and communities, both simply to the number of species and the functional diversity of those species; habitat and landscape heterogeneity; spatio-temporal diversity achieved by mobile organisms as they move through space; behavioural heterogeneity, achieved through dietary switching; meta-population diversity; and within-population or within-brood variation (i.e. diversified bet-hedging) (reviewed in Schindler *et al*., 2015). MacArthur (1955) and Elton (1958) were among the first to note that often, counter-intuitively, low biodiversity communities and simple food webs were more sensitive to environmental perturbations (Schindler *et al.*, 2015). Increasing the functional diversity of species within a community can increase the functional stability of that community over time, in the face of perturbations (Naeem and Li, 1997; Yachi and Loreau, 1999). This is sometimes called the "insurance hypothesis", and is a very specific example of portfolio effects operating at the community or ecosystem level, with emphasis on functionality[5]. Through each of these different avenues, variation can be introduced into the conditions which organisms experience, dampening out the potentially deleterious effects of extremes.

In spring-feeding caterpillars, one aspect of variability or unpredictability inherent in their niche is the point at which 'bud-burst' occurs. Not only is this a gradual, continuous morphological and biochemical process in and of itself (see Chapter 4), the nature of that process, its relative timing and rate of development will vary among different tree species, at different localities, growing under different environmental conditions, and between individuals (Cole and Sheldon, 2017). Before opening and during development, the buds of

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[5] In fact, use of the term "insurance" is probably misleading: "insurance does not affect risk, but rather transfers damage once it has occurred" (Schindler *et al*., 2015).

different species are inherently variable in their palatability to young caterpillars—I found that the buds of alder *A. glutinosa* and oak *Q. robur* were generally less usable by neonates across stages than, for example, birch *B. pendula* or sycamore *A. pseudoplatanus* (see Chapter 4). Plant species vary in both their thermal requirements for development, which often gives the *progress* of spring (i.e. bud-burst and leafing) a fairly sequential appearance across species (Lechowicz, 1984; Kramer, 1995; Roberts *et al.*, 2015), and in their phenological sensitives to temperature, meaning that temperature changes affect each species differently—this can extend, compress or disrupt that typical sequential leafing progression (Roberts *et al.*, 2015). Even across a site with identical conditions, then, the average onset of spring would be a patchy process that is, at least in part, determined by the specific composition and relative abundance of different species. We can see this even at a very small scale. Variation in phenological stage between different tree individuals growing very close together is often illustrated clearly by hawthorn (Figure 6.5). On sycamore, we can even see marked differences within an individual tree, with the buds in the exposed upper portion of the canopy frequently remaining closed while limbs in sheltered lower areas already feature large expanding leaves (Figure 6.5). In beech *Fagus sylvatica* bud-burst and unfurling seems to be fairly concerted, both within an individual tree and across trees at a site—on oak, in contrast, bud-burst is quite uniform within a tree but can vary greatly between different tree individuals (Figure 6.5).

Both genetic and environmental factors will influence variation in the phenology of different tree species and individuals. Of the latter, temperature conditions at the microclimatic level are likely to be particularly important in influencing differences within one (genetically homogenous) individual. Within a single tree, as well as between individuals, there are considerable temperature differences between micro-habitats (Nicolai, 1986; Prinzing, 2001; Kautz *et al.*, 2013; De Frenne *et al.*, 2021)—surface versus crevices in bark, lower versus upper limbs, shaded versus well-lit sides, etc. These micro-climatic differences will affect both tree and caterpillar development—when located on different parts of the same tree variation in temperature conditions could affect hatching times within a brood, perhaps driving match and mismatch at the scale of individual portions of the canopy. In the winter moth, for example, Hibbard and Elkinton (2015) found that eggs on the cool north-facing sides of tree trunks hatched on average 1.6 days earlier than those on the south-facing side. Across many Lepidoptera, microclimatic variation has been shown to be a significant factor in affecting

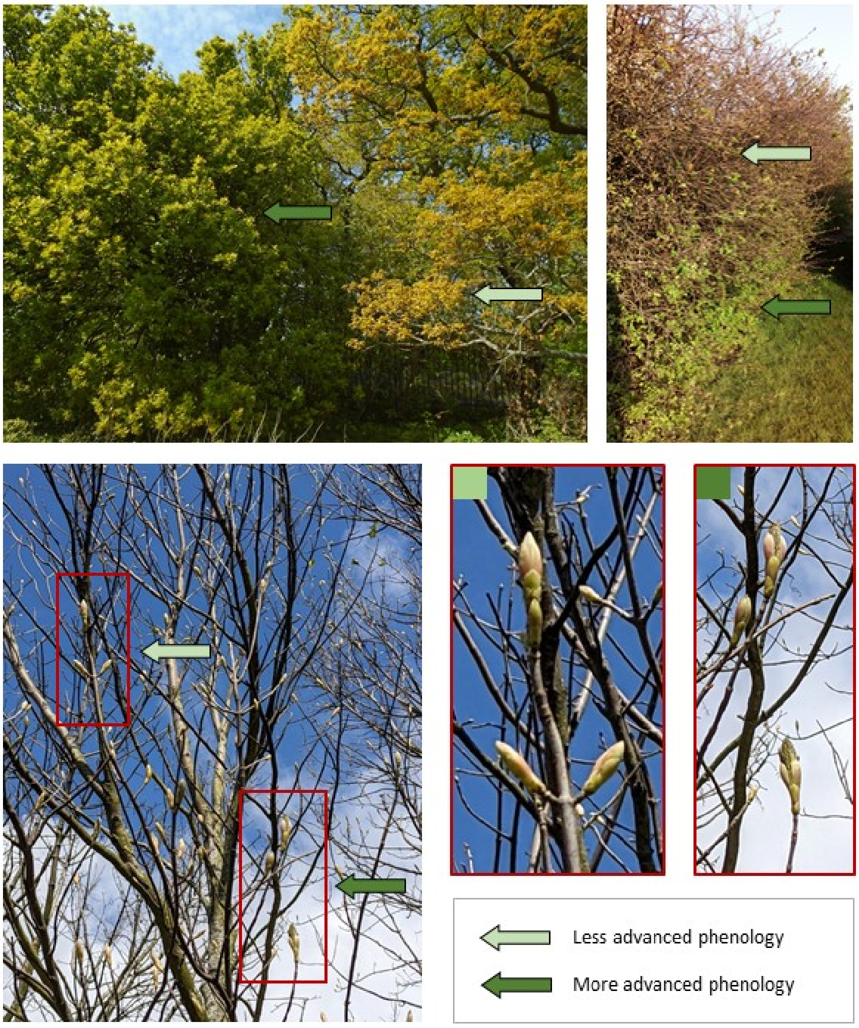

Figure 6.5. Local variation in the phenological development of different tree species. Such dramatic differences at a very small spatial scale highlight the extent of the uncertainty and unpredictability with which spring-feeding caterpillars must be able to cope. (a) Two adjacent oak trees *Quercus robur*, one fully in leaf and the other having only recently come into leaf (12 May 2019; Hermitage of Braid LNR, Edinburgh, UK); (b) A hawthorn hedge showing differences in leafing phenology between the top and bottom sections (17 April 2019; Falkirk, UK); (c) Differences in bud development between branches of a single sycamore *Acer pseudoplatanus* tree (2 April 2022; Culross, Fife, UK).

their development, persistence, and distribution (e.g. Davies *et al.*, 2006; Merrill *et al.*, 2008; Lawson *et al.*, 2012; Bennett *et al.*, 2015). Microclimate is a clear example of the importance of scale dependency (Levin, 1992) where, in aggregate across a site, we might see a shift in average temperature due to climatic changes, but at the very small scale in which most insects live their lives, there may be little change in the range or even average of temperatures experienced, or temperature fluctuations of a quite different kind (De Frenne *et al.*, 2021).

Variation and unpredictability in the spring phenology of different plants as well as microclimatic environmental variation in temperature could act to promote variation in caterpillar hatching phenology. Through the operation of portfolio effects, this variation in phenology buffers caterpillars at a population (and sometimes individual) level against asynchrony at a smaller spatial or temporal scale (Figure 6.4). Under changing future climatic conditions, the pool of genetic diversity generated by variability of this kind could be available for selection, allowing populations to adapt to the changes, while also serving to ameliorate the short-term effects.

6.7. Conclusions

Viewed as a fitness landscape for caterpillars, a woodland in spring can best be thought of as a dense and complex patchwork. We have many tree species with quite different underlying palatabilities, which respond to subtly different phenological cues, the foliage of which develop and mature at different rates—with a range of levels of within- and between-individual differences in each of these attributes—and which occur at various relative abundances. This complex structural environment creates a web of microclimatic conditions which serve to influence tree development as well as the rate at which caterpillar eggs develop over winter and into early spring. This heterogeneous environment will create a mosaic, at a very fine-grained level, of various degrees of match and mismatch between host and caterpillar phenology. Against this uncertain and variable environment, caterpillars come armed with adaptations which increase their resistance across a range of environmental conditions.

These buffering mechanisms take two broad forms: reducing the occurrence of asynchrony, or reducing the impact of it. Phenological plasticity allows caterpillars to broadly track the phenology of their hosts, minimising asynchrony. Polyphagy allows individual caterpillars to tolerate finding themselves on a range of host-plants. If they find themselves hatching too early they may bore into the developing buds of their host trees or endure short periods of starvation until food becomes available. Hatch too late and fitness does declines on older foliage, but not generally precipitously. If the situation appears dire enough, individuals can disperse, ballooning to a new and perhaps more propitious location. Nonetheless, this uncertainty promotes an evolutionary bet-hedging strategy, maintaining and even promoting a great deal of phenotypic variation in phenology. In sharp contrast to the typical view often taken at face value in the literature, of a group of species for which trophic synchrony is of crucial and overwhelming importance for fitness, we see instead, as a direct result of the variability and unpredictability inherent in their niche, a range of mechanisms which buffer populations against mismatch: not eliminating but ameliorating those negative effects.

Many of the buffering mechanisms which I have described here—starvation tolerance, generalist diets, bet-hedging phenotypic variation, etc.—are to be found very widely among other taxa, but hitherto little systematic attempt has been made to describe and classify them in this light. The concept of buffering unites these rather disparate traits and processes as drivers of stability in natural systems and environments. As the climate continues to change, understanding ways in which organisms and populations are able to tolerate environmental variation could not be more important. Not only that, but we can see more clearly the ways in which contemporary or historical environmental variation has been withstood and adapted to. Those mechanisms which have buffered populations against variation and unpredictability in the past may equally well serve to buffer at least some of the negative fitness consequences, in this case, of phenological mismatch induced by future temperature increases. Further, since it is the very vulnerability of these species to mismatch that must have driven the evolution of many of these buffering mechanisms, it may be, counter-intuitively, some of the systems which we view as most precarious under a changing climate that possess the greatest ability to tolerate variable conditions. If we wish to better understand the severity of climate change for natural systems, it is crucial that future research takes greater account of the ways in which such systems may or may not be buffered. How widespread this phenomenon is may dictate to a large extent the future resistance and resilience of many populations, communities, and entire ecosystems.

Chapter 7: General discussion and synthesis

7.1. Overview of key results

In a changing climate, divergent phenological responses across taxa have the potential to disrupt precisely timed interspecific interactions (Thackeray *et al.*, 2016; Burgess *et al.*, 2018; Cohen *et al.*, 2018). Where fitness is tightly linked with the degree to which one species can match the phenology of another species, a temporal decoupling of these interactions could prove catastrophic for the dependent population (Cushing, 1990; Durant *et al.*, 2007). Temporal decoupling of this kind, if widespread or occurring in keystone species, could undermine the stability of entire communities and ecosystems. But much remains to be understood. In this thesis, I aimed to specifically address several deficiencies in our understanding of the MMH, using the woodland tree/caterpillar/bird tri-trophic food-chain as a model system. This system has become one of the standard study systems for interpreting the interactions between climate change and the MMH (van Asch and Visser, 2007; Both *et al.*, 2009; Samplonius *et al.*, 2020). As an experimentally tractable ecological system, widespread throughout temperate environments, about which much is already understood, it is a good testing ground for these ideas. I have focused on the central link in that food chain—the caterpillars—which has received comparatively little attention, despite exerting significant top-down and bottom-up trophic effects. In regard to the MMH, only the winter moth *Operophtera brumata* has been considered at any great length by previous studies (see Chapter 3; e.g. Feeny, 1970; Tikkanen and Julkunen-Tiitto, 2003; van Asch and Visser, 2007; van Asch *et al*., 2007; Singer and Parmesan, 2010).

I have attempted to show that in relation to climate change and the MMH in this system, much of our practical and theoretical understanding rests on a very limited perspective of the biology of the species involved, and that we must return to and reconsider some of the key suppositions on which the MMH is based. A key precondition for the operation of the MMH is that the consumer species in the interaction relies on an ephemeral resource (Cushing, 1967). In Chapter 2, I considered this in the case of the winter moth, illustrating that it is actually highly polyphagous in its diet. Furthermore, it shows patterns of geographical divergence in performance across host-plant species, consistent with local adaptation but at a large spatial scale, such that this species may optimise its performance on regionally prevalent host-plants (for similar findings, see Kerslake and Hartley, 1997; Belsing, 2015). In Chapter 3, I directly assessed whether synchrony has a deleterious effect on spring-feeding caterpillars, covering a suite of six different caterpillar species (not just the frequently studied winter moth) on eight different host-plants. This performance assay, involving nearly 18000 caterpillars, is the largest such experiment to be conducted to date in terms of taxonomic scope and individual sample size, allowing me consider the extent to which we can generalise the effects of asynchrony across species. The effects of synchrony are typically considered to be severe, but I show that fitness declines rather gradually with increasing degrees of late hatching phenological asynchrony and these effects are contingent on the particular combination of caterpillar and host-plant species involved. Some are far more resilient in the face of mistiming than other species.

Previous work—including my experiments in Chapters 2 and 3—focuses largely on the consequences of hatching late, after buds have burst (see Chapter 3, Table 3.1). Comparatively little attention has been given to the fitness effects of caterpillars hatching too early, before buds have burst. In Chapter 4, I systematically investigated this for the first time. If they find themselves hatching too early caterpillars can either: disperse to a new location where food is available; wait it until it becomes available; or, make use of any (sub-optimal) material that is available on their natal host-plant. I demonstrated experimentally that caterpillars of the winter moth are able to bore into young, developing buds of various stages, as was suggested by earlier entomological authors (e.g. Stokoe, 1948), and thus exploit them as a food source should they hatch before leafing occurs. Furthermore, I show that caterpillars can often persist in the face of starvation, allowing them to simply wait for foliage to appear when they hatch early, though the extent of this ability can vary by a considerable margin across caterpillar species and environmental conditions, i.e. temperature. In Chapter 5, I focused on the early period of host-plant development, and considered how foliage maturation soon after bud-burst affects winter moth caterpillar development and growth rate. I found that development across three host-plant species in the early weeks after bud-burst has little effect on the performance of winter moth caterpillars, suggesting that the structural and biochemical changes which affect palatability occur later in leaf development (Feeny, 1970). I found evidence supporting the idea that caterpillars feeding on sub-optimal hosts may adjust the rate of their development to compensate for this, and escape these stressful conditions (Stamp and Casey, 1993). There was substantial variation in caterpillar performance between moth broods and between individual trees, which is consistent with the hypothesis that variation in caterpillar phenology is a diversified bet-hedging strategy. In summary, across Chapters 2 to 5, I found that, contrary to the typical story portrayed in much of the literature, spring-feeding caterpillars are in fact buffered to a surprising extent in the face of variation in their environmental conditions—indeed, this may have developed out of the inherent uncertainty of the temporal niche which they occupy.

Finally, in Chapter 6, I discussed and formalised the concept of *buffering*, a term widely used in the phenological and ecological literature (e.g. Roland and Myers, 1987; Yachi and Loreau, 1999; Burgess *et al.*, 2018; Wang *et al.*, 2020; De Frenne *et al.*, 2021; Iler *et al.*, 2021) but which has hitherto attracted little theoretical consideration. Using the spring-feeding caterpillar guild as a case study, I explored the mechanisms which act to maintain the stability of organisms under variable environmental conditions, and considered how these may also ameliorate any negative effects of novel environmental changes such as climate change. I considered how a natural propensity to withstand the environmental uncertainty or unpredictability inherent in many ecological situations could impart resilience, among at least some groups of organisms, in the face of these predicted climatic changes.

7.2. Does synchrony matter in spring-feeding caterpillars?

7.2.1. Peaks, pulses, and plateaus

In order to project how spring-feeding caterpillars (and the species with which they interact) will be affected by climate change, we have first to understand the range of environmental conditions which they typically experience and the adaptations and strategies they employ to cope with that niche—the importance of changes can only really be assessed relative to a historical baseline (Kharouba and Wolkovich, 2020). As I have discussed in Chapter 6, spring-feeding caterpillars face an extremely variable and uncertain environment. The structure, specific composition, and hence, phenological profile of a woodland in spring (i.e. the temporal occurrence of the caterpillar’s key resource: newly flushed leaves) are highly heterogeneous, both spatially and temporally. Limited adult dispersal and microclimatic heterogeneity, among other factors, mean that caterpillars could find themselves in any number of a diverse combination of different biotic or abiotic situations, which may differ greatly from those experienced by their parental generation. Because of an inability to accurately predict which plant, or even species, they will find themselves on, adaptive fine-tuning of caterpillar phenology to match that of their host-plant is likely greatly hindered (though cf. Dongen *et al.*, 1997)—nor are microclimatic environmental cues necessarily reliable predictors of host phenology in any case, due to genetic differences in the phenological sensitivity to temperature and microclimatic variation across an individual tree. Caterpillars cannot predict, therefore, the extent to which they will be synchronous with nearby foliage. Against this unpredictability, inherent in the spring-feeding niche, caterpillars deploy a range of mechanisms which allow their populations to persist (see Chapter 6).

The onset of spring does not occur rapidly and in concert, but is gradual, cumulative, and spatially heterogeneous—it is best conceptualised across a landscape as a patchwork. The *window of opportunity* (Hunter, 1993; Diss *et al.*, 1996; Schwartzberg *et al.*, 2014; Falk *et al.*, 2018; Fuentealba *et al.*, 2018) for spring-feeding caterpillars, therefore, is equally protracted, heterogeneous, and patchy: different host-plants, and different parts of the same individual host-plant, each varying in their inherent palatability, developing at their own rate, and with their own distinct microclimate. At a very high resolution—at the level of the individual—the temporal fitness peak associated with hatching time is indeed fairly sharply defined, because that caterpillar finds itself in one particular patch of the phenological landscape. In this situation, individual caterpillars possess adaptive or plastic traits which act to minimise the effects of any mismatch: they may feed on a broad range of species, can tolerate periods of starvation or disperse when food is unavailable, bore into unopened buds, or consume mature foliage (though fitness still declines in each case) (Chapters 2, 3, and 4).

The coarser our resolution of the environment, the broader, and less sharply-defined, that fitness landscape becomes. Among the offspring of a single individual, we see diversified bet-hedging and portfolio effects—phenotypic variation in individuals ensures that in these unpredictable conditions at least some will persist (Chapter 6). Across a population, and the caterpillar guild, these same processes act a larger scale—individuals are spread across a range of different environments, such that there is reduced variation in mean fitness across generations in the population, at the expense of increased variation within any given year.

Under natural conditions, then, and viewed from the perspective of the spring-feeding caterpillar population, the window of opportunity during which foliage is available for exploitation is in fact less a sharply-defined peak—as it is often portrayed in the literature (see Chapter 3, Table 3.1; Feeny, 1970; Tikkanen and Julkunen-Tiitto, 2003; van Asch et al., 2007)—and more a broad and flat, plateau-like resource *pulse*, occurring across a fairly protracted time period (Figure 6.4). Even at the level of individuals, or their offspring, buffering mechanisms act to flatten this peak out and generate a more gradual fitness profile.

On the evidence I have presented here it seems clear that, for spring-feeding caterpillars, synchrony does matter for fitness, but it does so within broad temporal bounds—at a scale of weeks and months, not days (Chapter 3). Indeed, it seems likely that the inherent variability in that fitness landscape (the patchiness I have described above) means that asynchrony could not feasibly exert such severe consequences and caterpillar populations still persist, or attain the sizes we can see in the field. Some of the discrepancy between the evidence presented here and in other studies may be attributable to large sections of the literature having tended to focus on single caterpillar/host interactions, particularly winter moth on English oak *Quercus robur*.

7.2.2. The exceptions and the rules

We are slaves to study systems—they make broad questions testable but are, of necessity, a unique set of biological circumstances. The difficulty comes in determining the limits that a particular system imposes on the extent of our generalisations from it. As we have seen, literature on temperate spring-feeding caterpillars, and particularly literature relating to the MMH in the tree/caterpillar/bird food chain, is dominated by the winter moth (van Asch and Visser, 2007). For higher trophic levels in this system which view spring-feeding caterpillars as an ephemeral food source, winter moth is often taken as representative of the entire guild (see Section 1.4.1). Certainly, this species is often disproportionately abundant in the field among the spring-feeding caterpillar assemblage (Feeny, 1970; Kulfan *et al.*, 2018; Shutt *et al.*, 2019a), and is of considerable ecological and economic importance (Briggs, 1957; Elkinton *et al.*, 2014a). However other species can equal or exceed it in abundance, depending on locality and habitat (Hunter, 1992). The literature (Tikkanen and Julkunen-Tiitto, 2003; van Asch *et al.*, 2007) and my own experiments (Chapter 3) suggest that winter moth caterpillars are affected strongly by phenological mismatch, and therefore that increased mismatch in future, occurring due to climate change, threatens their persistence and the fitness of higher trophic levels which depend on them. But how typical is the winter moth of other spring-feeding species?

Beginning with the entomologists of the nineteenth century, research on spring-feeding caterpillar species was initially concerned with their fundamental natural history and, later, explaining temporal patterns of species occurrence. Why do some caterpillars feed in spring and others not? Why do many of these spring-feeding species feed only then? This question was perhaps most famously addressed by Feeny (1968, 1970), who used the winter moth populations at Wytham Wood in Oxford, an oak-dominated site, as a study system. Feeny hypothesised that the accumulation of plant defences in spring and early summer delimited a period during which the foliage of many plants was 'apparent' (Feeny, 1976)—i.e. available for utilisation because it was of acceptable palatability, to an extent which it would not be later in the year. In many ways this represented a parallel development of the ideas explicitly formalised by Cushing (1967, 1969, 1975, 1990) as the MMH. Feeny's work became the bedrock of a literature focusing on spring-feeding caterpillars as an example of the MMH operating in a terrestrial environment, and a system in which to consider how the incidence and severity of mismatch could be affected by climate change, using winter moth caterpillars and oak as model species (see Chapter 2, Tables 2.1 and 2.2; Chapter 3, Table 3.1). Thus, it seems that the somewhat myopic focus on this particular species pairing as representative of the wider system is largely a result of historical and geographical coincidence.

Although both winter moth and oak are widespread and prevalent species, they appear to be in fact rather atypical in terms of the effects of mismatch on their fitness and palatability, respectively. In Chapter 2, I found that across four British populations winter moth caterpillar fitness on oak is among the lowest of all the host-plants trialled (see also Cuming, 1961; Wint, 1983; Kirsten and Topp, 1991; Tikkanen *et al.*, 2000; Tikkanen and Lyytikäinen-Saarenmaa, 2002; but cf. Vanbergen *et al.*, 2003; O'Donnell *et al.*, 2019). Overall, it seems that fitness can vary at a large spatial scale on different host-plants, and where oak is less prevalent, caterpillars perform less well on it (e.g. Kerslake and Hartley, 1997). Nonetheless, even in Britain, where oak is fairly common, there are still other abundant, widespread host-plant species on which winter moths perform at a far higher level—for example, birch *Betula* *pendula*, a common understory and scrubland tree (see Chapters 2 and 3). With increasing asynchrony, performance on oak reaches a lower level more rapidly than on many other host-plants (see Chapter 3, Figures 3.6-3.8). Winter moth caterpillars too are among the worst performers—relative to other well-known out-breaking species such as the gypsy moth, their ability to tolerate starvation is very low, on the order of several days, even at low temperatures conducive to survival (see Chapter 4, Figure 4.2). Winter moth performance across host-plants starts at low levels relative to other species, and declines at a more rapid rate with increasing asynchrony—for example, by hatching thirty days asynchronously, the probability of survival of winter moth caterpillars approached zero on almost all host-plants, whereas in other caterpillar species it remained between 25-50% (see Chapter 3, Figure 3.6). Considering different caterpillar by host-plant combinations we find the estimated fitness of winter moth caterpillars on oak substantially lower than on other host-plants (see Chapter 3, Figure 3.9). Winter moth caterpillars are significantly less able to utilise unopened oak buds as food, relative to other host-plant species (see Chapter 4, Figure 4.4).

The extent to which synchrony matters, therefore, for caterpillar fitness depends to a high degree on the particular species pairing involved. Widespread focus on a very narrow study system certainly has the potential to mislead, and there is a clear suggestion from evidence presented here and elsewhere that the trophic interaction between winter moth and oak is not typical. Biological and ecological assumptions developing out of this system should therefore be considered carefully, and we should certainly exercise caution when attempting to generalise from these species in particular to their respective guilds, or more widely to other taxonomic groups. This must particularly be borne in mind if we wish to understand and pick apart the potential effects of climate change on entire ecosystems, and large-scale impacts on mismatch, population-level fitness, and the cascading effects through other trophic levels.

7.2.3. Spring-feeding strategies

The accumulation of late season plant defences (both structural and biochemical) makes foliage increasing unpalatable for phytophagous insects in spring, delimiting their window of opportunity for feeding (Feeny, 1970, 1976; Tikkanen and Julkunen-Tiitto, 2003; Smilanich *et al.*, 2016). These defences do not, however, make feeding impossible later in the season—

there are many species which feed exclusively in this period (Maitland Emmet and Heath, 1992; Henwood *et al.*, 2020)—but it involves investment in an apparatus of physiological and morphological adaptations to overcome the defences (Schoonhoven *et al.*, 1998). In the winter moth, rather than deal with the anti-herbivory defences built up as leaves mature, individuals gamble on matching the phenological window within which the energetic investment in these adaptations is not required, so as to maximise their fitness. This highlights the importance of trade-offs in this system. Spring-feeding caterpillars, such as those of the winter moth, are adapted to a narrow phenological niche, avoiding the need to invest in combating late season plant defences, but at the cost of dealing with the inherent unpredictability and uncertainty of this niche (see Chapter 6). Early spring-feeding caterpillars typically have a broad diet (Maitland Emmet and Heath, 1992), generally tolerate starvation to an extent greater than many late season species (compare Chapter 4 with e.g. Reavey, 1992), can disperse to new hosts, and adopt various bet hedging strategies (see Chapter 6). They therefore seem to *compensate for their narrow phenological niche by having a broad, generalist trophic niche*; by being robust to uncertain environmental conditions. Late season species can afford to be more host-specific, for example, or have lower thresholds of starvation tolerance, because (although that resource is itself more difficult to utilise) there is far less uncertainty in the *availability* of that resource when they do indeed hatch.

The extent to which the “spring-feeding caterpillar guild” is a cohesive unit is, however, open to question—it is a useful grouping but not a rigid one (see Figure 1 in Feeny, 1970). Some of the species studied in this thesis, such as the vapourer *Orgyia antiqua* and scarce vapourer *O. recens*, produce several generation each year, the first of which feeds in the earliest part of spring as the buds break, and the others feeding later in the season, on mature foliage (Skinner, 2009; Porter, 2010; Waring *et al.*, 2017; Henwood *et al.*, 2020). Perhaps it is not surprising then that I find that these species are among the least affected by asynchrony—on many host-plants, survival probability does not begin to decline in the vapourer until hatching occurs well over 40 days after bud-burst (see Chapter 3, Figure 3.6). It is possible in such species that later generations plastically respond to late season plant defences, but this requires further research. Indeed, in other *Orgyia* species, a diet of mixed age foliage has been shown to be optimal (Johns *et al.*, 2009). The consistently high levels of performance across host-plant species and with various degrees of asynchrony leads us to wonder why these species are not more common in the field than those which are comparatively far more susceptible to the negative effects of asynchrony, such as the winter moth and mottled umber (see Chapters 3 and 4). Certainly, in spring woodlands, the caterpillars of these latter two species far outnumber the vapourer, as do the adults in their appropriate season. Vapourer moths have even more limited dispersal than the adult female winter moths—while male vapourers are capable of flight, the females are so large that they do not move far from their cocoon, which is spun on the bark of their host-plant (Majerus, 2002). The males typically mate with them before they have fully eclosed or immediately afterwards. The females then lay their eggs on the surface of their old cocoon and pupa (Majerus, 2002). This extreme lack of adult dispersal may have promoted investment in even greater resistance to asynchrony than we see in other spring-feeding species.

The gypsy moth and black arches have their own variations on the typical life history of the spring-feeding caterpillar species. Although univoltine, females are fully winged and are active in the summer months (Waring *et al.*, 2017). This makes host-plant discrimination and choice a more viable behaviour for them, potentially allowing them to increase the fitness of their offspring by selecting the optimal hosts in any given situation. The caterpillars of these species, particularly the black arches, are also far more robust to asynchrony than winter moth, for example—they have a far greater tolerance of starvation (see Chapter 4) and ability to utilise maturing foliage when they hatch late (see Chapter 3), particularly within the initial three or four week period following bud-burst. This may, in part, be due to their larger size—some of the difficulty in consuming more mature foliage may be due to its becoming biomechanically tougher which makes it increasingly difficult to chew (Feeny, 1970; Hanley *et al.*, 2007). The neonate caterpillars of the gypsy and black arches moths are much larger (Author, personal observation) and may not be similarly inhibited.

Even within those caterpillar species which are exclusively early season feeders, we can see the importance of trade-offs emphasised in the juggling of different adaptations and behaviours required to fill specific niches. A good contrast is to be found between the winter moth and the green oak tortrix *Tortrix viridana*, another species with populations that undergo periodic and extreme fluctuations in size (Hunter *et al.*, 1997). Although the eggs of both species hatch just as the buds are breaking in spring time (Waring *et al.*, 2017; Langmaid *et al.*, 2018; Henwood *et al.*, 2020), in contrast to the highly polyphagous winter moth caterpillars, the caterpillars of the green oak tortrix feed predominantly on oak[6]. Because of this increased host specificity, dispersal as a small caterpillar via ballooning would be a riskier strategy than in the winter moth (radical versus conservative searching, see Jones, 1977). When they hatch too early, the neonate caterpillars of the green oak tortrix display dispersal behaviour at a substantially lower rate than those of the winter moth (Hunter, 1990) but they have a much greater tolerance of starvation, approximately 25 days versus 8 days at 8°C, for example (Hunter, 1990). During this time, it is likely that buds on their host tree will break and foliage will become available for them to utilise. Additionally, at the population-level, among individual variation in caterpillar hatching date within a given year mirrors closely among individual variation in the timing of oak bud-burst (Ivashov *et al.*, 2002), suggestive of a diversified bet-hedging approach (see Chapter 6). Relative to the winter moth, therefore, we see yet another rebalancing of trade-offs—starvation tolerance emphasised at the expense of polyphagy to facilitate host-plant specialisation.

Although sharing many common approaches to dealing with the problems inherent in their broader niche, spring-feeding caterpillars are nonetheless ecologically and evolutionarily diverse. As such, understanding how the MMH operates in this system, and what impacts the phenological effects of climate change might have on their populations, the structure of their communities, and the stability of their biotic interactions, necessitates a far broader research approach than has hitherto been adopted—one which takes account of the diversity of these species and their approaches. This study is the most taxonomically broad experimental assay to date testing the fitness effects of asynchrony (see Chapter 3, Table 3.1), but to understand the biological traits underlying these differences in performance, beyond the simple discussion posed here, would require a phylogenetic comparative analysis across a far greater number of species.

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[6] Reminiscent of the case of the winter moth (see Chapter 2), the literature typically describes the green oak tortrix as monophagous on oak. In fact it has been recorded feeding on a number of other deciduous trees in nature and in captivity (Robinson *et al.*, 2010), although it is well established that this occurs far more rarely than polyphagous feeding in the winter moth (Maitland Emmet and Heath, 1992).

7.2.4. Should we expect synchrony in the field?

To expect to find synchrony between caterpillars and their host-plants in the field as the default state we must make two assumptions. The first is that caterpillars are able to adaptively track the phenology of the host-plant *individual* on which they will find themselves (Dongen *et al.*, 1997). This I have already discussed (see Chapters 2 and 3) and consider to be unlikely other than in exceptional circumstances, although they do show phenological plasticity broadly analogous to that of trees at a population or community level (Visser *et al.*, 2006; Charmantier *et al.*, 2008; Both *et al.*, 2009; Burgess *et al.*, 2018). In fact, we see a variety of buffering mechanisms to cope with various degrees of trophic mismatch, alongside diversified bet-hedging strategies to spread risk among individuals through within-population and within-brood variation in phenology (Chapter 6). The second assumption required if we are to expect synchrony to be the default state in the field is that the selective disadvantage of hatching late is equal and proportionate to that experienced when hatching too early. Although some authors have estimated such a symmetrical relationship (van Asch *et al.*, 2007), others find it skewed so that early hatching is more costly than hatching late (Tikkanen and Julkunen-Tiitto, 2003). This latter assumption would seem to be supported by my results, where the probability of establishment on opening buds increases rapidly as they develop (Chapter 4), but fitness declines more slowly as foliage ages (Chapter 3). In this manner, the fitness profile could follow an escarpment-like shape across time—a relatively steep increase in fitness followed by a more or less gradual tapering off as leaves and foliage age (see Figure 6.4 for an illustration). These unequal selective pressures could result in the mean phenology of a caterpillar population being asynchronous with the mean phenology of the host-plant population, even though caterpillar fitness is optimal when perfectly synchronous (Singer and Parmesan, 2010).

Adaptive asynchrony could also arise through life history trade-offs: for example, if early hatching impacts fecundity but late hatching impacts survival, these impacts are not likely to be balanced (though cf. Hunter and Elkinton, 2000; van Asch *et al.*, 2007) and so, once again, the mean phenotype of a population would be asynchronous, despite fitness being maximised by synchrony (Singer and Parmesan, 2010). In addition, ongoing phenological arms races between host-plants and their consumers (see Appendix 5) will also tend to produce asynchrony, as plant phenology is pushed into "enemy-free time" (Singer and Parmesan, 2010). These effects are extremely important, because they delimit the historical baseline from which we can make comparisons about the effects of modern climate change—assuming that populations were synchronous in the past, and that they have been pushed into asynchrony by recent climatic changes may be inaccurate, and could perhaps lead us to infer that these systems are more fragile than they actually are.

In the field, studies on the winter moth find a range of different levels of synchrony with host-plants (oak, in this case) under natural conditions. Van Asch and Visser (2007) report that across the period 1990-2005 caterpillar hatch in a Dutch population occurred consistently before bud-burst on oaks, by around 10 days on average. Similarly, Buse and Good (1996) found that in a population in northern Wales mean hatch date generally preceded that date of bud-burst, but by a much smaller margin. Buse *et al.* (1999) conducted experiments in artificially heated solardomes to simulate ambient temperatures and projected global warming—under both treatments, they found that caterpillars hatched synchronously with their host-plants. Furthermore, the evidence that caterpillars are responding more strongly to climate warming than their hosts is mixed, and the trends may vary by geographical location (Charmantier *et al.*, 2008; Both *et al.*, 2009; Thackeray *et al.*, 2016; Burgess *et al.*, 2018; Macphie *et al.*, 2022). It is a feasible scenario, therefore, that under climate warming the relative synchrony between host-plants and caterpillars might not change, but we (as researchers) may come along and quantify the phenology of both trophic levels in a given population and assume, incorrectly, that it has been disrupted by climate change, not realising that it is by default asynchronous. This demonstrates the importance of understanding the broader biology of any given system before making long-term predictions or prognostications about the effects of environmental changes, and also the crucial need for long-term datasets where historical baselines for phenological comparisons have been established (Kharouba and Wolkovich, 2020).

7.3. Does synchrony matter at all?

7.3.1. Climate change and phenological asynchrony in theory and in practice

The extent to which the MMH operates in any system depends on the degree to which that system conforms to a range of criteria, first articulated clearly by Cushing (1990; though see also Durant *et al.*, 2007; Samplonius *et al.*, 2020; and Section 1.2). Indeed, the MMH was developed within a specialised marine biological context (Hjort, 1914; Cushing, 1967, 1969; see Appendix 4), and it is still unclear the extent to which it generalises beyond some very specific ecological scenarios. I find it particularly difficult to reconcile the assertions: that phenological synchrony occurs widely in a range of communities and ecosystems; that mismatch can exert very strong selective effects; and, that such synchronised systems are easily driven to mismatch by environmental or climatic variation or change This is essentially the view often taken in the case of spring-feeding caterpillars (e.g. Chapter 4, Table 4.1)—mismatch has catastrophic effects on fitness, and it can be easily induced. For instance, van Asch and Visser (2007) write that:

> “The degree of synchrony can vary strongly between years. This variation provides direct evidence that the underlying mechanisms respond differently to environmental conditions, even though the mechanisms determining insect herbivore phenology is selected to mimic as closely as possible the response of the host plant”

It seems contradictory that on the one hand we have extremely strong selection for as great a degree of synchrony as possible with the host-plant, while on the other we have intrinsically divergent phenological responses to variation in environmental conditions between these taxa. If selection for synchrony is so great, if species or trophic levels depend on each other to such a large extent, why do they not match one another *more closely* in their phenological sensitivities to temperature (see Section 1.2 and 1.3.2)? The environment is variable and constantly changing, over a range of spatial and temporal scales, and if two synchronised species, a pollinator and a plant for example, showed different phenological responses to this change then they might not persist. In short, if the MMH operated pervasively across ecosystems then we might reasonably expect a closer convergence of the phenological sensitivity to temperature across trophic levels. In fact, observed phenological changes over the last few decades have varied among trophic levels and taxonomic groups (Thackeray *et al.*, 2016; Roslin *et al.*, 2021), and asynchrony has increased between many interacting species pairs by up to 10-15 days/decade (Kharouba *et al.*, 2018). With strong selection against mismatch, we might reasonably expect population or even ecosystem-level collapses with such degrees of asynchrony, but do not seem to find this. In other words, if a sensitivity to mismatch rendered such species so vulnerable to environmental variation how do their populations persist?

Phenological synchrony is only one aspect of the ecological context in which a species exists. The extent to which synchrony is important will vary depending on the degree to which a given system conforms to the basic criteria for the MMH to operate: a temporally ephemeral resource, and fitness which varies depending on synchrony. There are gradations of vulnerability between species to mistiming, degrees of dependency of one species upon another, and a continuum of susceptibility to the negative effects of mismatch—this will affect the potential significance of increased mismatch resulting from future climate change. In situations, such as we see in the case of spring-feeding caterpillars, where both of these basic criteria theoretically hold but where there are reasons why it is difficult for consumers to perfectly track the phenology of their hosts (e.g. environmental variation, the phenological arms race [see Appendix 5]; see also Reed *et al*., 2010), then buffering mechanisms are likely to arise, ameliorating the fitness effects of inevitable mismatch. By extension, species that exist within a phenologically variable or unpredictable environmental context are more likely to possess some degree of intrinsic robustness to climate change induced disruptions of their phenology, and that of the species they rely upon. In some very specific instances, match or mismatch may be a highly significant determinant of future success, but I would argue, based on this reasoning, that it is not likely to be generally the case.

7.3.2. The winter moth as an invasive pest

The expanding distribution and invasive status of the winter moth in North America is a powerful piece of evidence which would seem to contradict its apparent susceptibility to mismatch (see Chapter 3). The winter moth and the northern winter moth *O. fagata* are native and widespread in the Palaearctic (Skinner, 2009; Waring *et al.*, 2017), with sister species which parallel them in North America (*O. bruceata* and *O. danbyi*) (Troubridge and Fitzpatrick, 1993; Beadle and Leckie, 2012). On three separate occasions, however, the winter moth has been introduced to North America: Nova Scotia in the 1930s, Oregon in the 1950s, and Vancouver in the 1970s (Hawboldt and Cuming, 1950; Cuming, 1961; Embree, 1965; Ferguson, 1978; Gillespie *et al.*, 1978; Kimberling *et al.*, 1986; Simmons *et al.*, 2014). Consistent with the population bottlenecks arising from these events, genetic diversity in the winter moth population relative to endemic North American *Operophtera* species is low (Gwiazdowski *et al.*, 2013). Despite in each case facing a climatically distinct habitat and an entirely alien suite of host-plant species, the winter moth has spread rapidly following these introductions. From its arrival on Vancouver Island ca. 1972, the species has spread over an estimated 120km on the island and neighbouring mainland areas. From Oregon, it has spread into Washington State, several hundred kilometres away (Troubridge and Fitzpatrick, 1993). From Nova Scotia, it has spread hundreds of kilometres into the surrounding states and territories, in the North-Eastern United States and Ontario (Elkinton *et al.*, 2010, 2014a, 2014b). Elkinton *et al*. (2014) monitored New England populations and found that they expanded their range westwards in Massachusetts by 44km over a period of six years. In each case, the initial introduction was followed by long-term outbreaks and infestations, which were subsequently controlled by introduced parasitoid species (Gwiazdowski *et al.*, 2013).

If phenological synchrony were so fine-tuned and important, how could this species have persisted and spread at such a rapid rate in novel environments, woodlands, and on novel host-plant species? Despite female flightlessness, dispersal is clearly possible via larval ballooning (Edland, 1971; Legget *et al.*, 2011) though, notably, this could act against local adaptation to tree or mean stand phenology, potentially exacerbating asynchrony. The fact that long-term outbreaks are rapidly brought to an end by the introduction of parasitoids (Gwiazdowski *et al.*, 2013) also highlights the relative importance of antagonistic biotic interactions, relative to mismatch, in determining the success of this species, and also perhaps in affecting periodic fluctuations in population size (Varley *et al.*, 1974). The history of biological invasions by the winter moth may provide us with an example of how synchrony could be an important, but overestimated, ecological factor.

7.3.3. Buffering in the woodland food-chain and the generality of mismatch

Synchrony is also important for other species and trophic levels in the tree/caterpillar/bird spring food-chain. Trees must break their buds at an appropriate time, so as to avoid damage due to inhospitable weather conditions but also to maximise use of growing conditions (Lenz *et al.*, 2016). Birds must lay so that their chicks hatch when the optimal food supply is available, at the height of the “caterpillar peak” (see Section 1.3.1). The caterpillar peak is comprised of a number of different spring-feeding caterpillar species (Feeny, 1970; Kulfan *et* *al.*, 2018; Shutt *et al.*, 2019a), which differ in their ecological requirements (Maitland Emmet and Heath, 1992; Henwood *et al.*, 2020), vary in abundance between habitat types, precise phenological patterns, and phenological sensitivity to temperature. Different caterpillar species may also vary in their nutritional value to prospective bird consumers (e.g. Samplonius *et al.*, 2016). Differences in the composition of the caterpillar fauna of a woodland site, then, could affect the phenological profile of the caterpillar peak (as illustrated in Figure 6.4 for caterpillars and their host-plants), which in turn will modulate the costs of mismatch for birds as secondary consumers. In a similar manner to the heterogeneous nature of a woodland buffering caterpillar populations from mismatch via portfolio effects, variation in the composition of the caterpillar peak could act to buffer passerine bird populations.

Indeed, we can find many buffering mechanisms among the bird component of this food-chain which are analogous to those I have described at length in the winter moth and other spring-feeding caterpillars (see Chapter 6). Birds can be fairly robust to changed environmental conditions when breeding, and perform well even when translocated to different sites (Burger *et al.*, 2013). Although there may be a great deal of genetic control involved in lay date among early spring breeding species such as tits and flycatchers (Visser *et al.*, 1998; Both and Visser, 2005), breeding could also be stimulated directly by the presence of food supplies (Perrins, 1991; Chmura *et al.*, 2020). To buffer their offspring against changing conditions in the unavoidable time lag between lay date and hatching (e.g. if conditions suddenly improve and the timing of the caterpillar peak advances), birds can plastically adjust the incubation period of their eggs and thus the time they hatch (Simmonds *et al.*, 2017). Across bird species, dietary requirements vary (Betts, 1955; Dhondt, 1977; Perrins, 1991) which, as in the case of the caterpillars, could give rise to interspecific differences in the effects of mismatch.

An often ignored factor which, because of their life history, is not so likely to operate in caterpillars but which may be more significant for other taxa is that species may be buffered against mismatch by the abundance of the resource peak they are tracking (Durant *et al.*, 2005)—Cushing (1990) noted that in marine systems mismatch was more likely in years of low resource abundance than in high abundance years, where the height of the peak effectively minimises mismatch with any given quantity of temporal asynchrony. While the evidence is mixed, there is a suggestion that although the caterpillar peak occurs earlier in warmer years it may also be taller, which could buffer the populations of secondary consumers against any resulting phenological asynchrony (depending on how the width of the peak is affected; Macphie *et al.*, 2022). Indeed, in years where caterpillars are more abundant overall, clutch size is greater in tits (Perrins, 1965, 1991; Both and Visser, 2005). In pied flycatchers Visser *et al*. (2015) found that asynchrony did not affect the strength of selection for synchrony but the height of the caterpillar peak *did* affect fledgling success: "the lack of an effect of synchrony could thus be partly obscured by variation in caterpillar peak height". We see similar trends in other groups: Durant *et al.* (2005), for example, found that in three different trophic systems (fish/plankton, seabird/fish, and sheep/grass) abundance significantly influenced the effects of asynchrony, suggesting that it may be an important mediator of mismatch in the field.

The occurrence of various buffering mechanisms across trophic levels in this system indicates the extent to which they may occur more widely, in other communities and taxonomic groups. Future workers considering purportedly phenologically synchronised systems, and the impacts of climate change, would do well to take account of ways in which organisms may be buffered before making projections as to possible changes in their populations.

7.4. Some key limitations of this thesis

Despite the size and scope of the experiments presented here, several methodological constraints are worthy of more detailed consideration. Captive rearing experiments in general involve a trade-off between replicating a natural situation and standardising experimental conditions. Here, caterpillars were reared in cultures at controlled temperatures and fed excised foliage collected in the field. Foliage was refrigerated to keep it fresh but it is certainly possible that after collection it may have become slightly desiccated (though steps were taken to minimise this) or undergone other biochemical changes affecting its palatability—and thus the extent to which my results are reflective of a natural situation. The alternative, however, of rearing caterpillars on living host-plants would introduce systematic microclimatic and environmental differences between individual treatments and host-plant species. Despite rearing on excised foliage, the results I have obtained here for individual host-plants are in most cases not far removed from those in other, methodologically diverse studies (see

Chapter 3, Table 3.1; compare Chapters 2, 3 and 5), suggesting that such differences as do exist are due largely to treatments and not the confounding effects of experimental design. If anything, survival is in many cases *higher* here than in other studies, and if excision affected palatability we would expect logically to see a decline in fitness.

It was a key aim of this thesis to establish the extent to which the effects of asynchrony and mismatch in the winter moth/oak pairing could generalise across other spring-feeding caterpillar species. I have shown that substantial and significant differences do exist in the response to asynchrony between different caterpillar and host-plant species (see Chapters 3 and 4). To increase the extent to which we could generalise from these results, it might be useful to quantify asynchrony in terms of a growing degree day model (e.g. Tikkanen and Lyytikäinen-Saarenmaa, 2002; Tikkanen and Julkunen-Tiitto, 2003), rather than calendar days (e.g. van Asch *et al.*, 2007)—this could allow the results to be employed for generating predictions under changing field conditions.

Most experiments attempting to assay the fitness of caterpillars use one of a fairly small number of metrics (see Chapter 5, Figure 5.1). Here, I measured three principal metrics which have obvious fitness implications, and computed a fitness measure for the winter moth from two of these (survival and pupal mass). Under challenging conditions, insects can employ various compensatory feeding mechanisms, modifying their developmental rates, growth rates, feeding rates, etc. (Stamp and Casey, 1993). In the context of the MMH, these abilities have not been investigated fully as potential physiological and behavioural buffering mechanisms, and would repay future consideration. Here I only dealt with this in a very limited way, quantifying development time in each treatment group. But it is not immediately obvious how to integrate development time into our estimates of treatment group fitness (as I have discussed at length, see Section 3.4.5 and Chapter 5). A protracted period of development as a caterpillar, for example, may expose an individual to greater risk of predation. Rearing caterpillars in the lab is a good way to isolate the specific fitness effects of host-plant palatability, but we must remember that this is only one factor contributing to fitness. In other words, in the field there are other environmental variables to consider, some of which may be host-plant specific, and which may modify the outcomes we might expect based on the palatability of the hosts alone. Predation or parasitism pressure may be higher on some plant species—trees such as oak with layered, overlapping leaves might prove

Figure 7.1. Larval feeding structures and damage of the winter moth *Operophtera brumata* on cherry *Prunus* sp. Caterpillars spin leaves or parts of leaves together using silk, particularly visible in (a), to create a more sheltered structure within which to feed. This may offer them some protection from predators and adverse environmental conditions. Thus, the morphology and growth patterns of different tree species could make them particularly conducive, or not, for the spinning of these structures.

themselves more conducive to larval spinnings (Figure 7.1), in the winter moth for example, and provide the caterpillar with more protection from weather conditions or predation, than would a tree with a more open structure, like birch, exposing caterpillars to the elements. Predators or parasitoids may be more or less associated with certain species of host-plant (Gibb, 1954; Partridge, 1974; Holmes and Robinson, 1981; Ohsaki and Sato, 1994). Here, I find that survival on oak is very low compared with birch, but if predation pressure on birch is far higher (Chapters 2 and 3), this could entirely outweigh the fitness effects of palatability-determined survival. It is therefore important that future work attempts to marry these different contributors to fitness in the wild together.

Similarly, there is the possibility that conflicting selection pressures at different life history stages could modulate my results in the field. Pupal predation in the winter moth, for example, has been shown to be a significant cause of mortality (Varley *et al.*, 1974; Hunter *et al.*, 1991). While it is largely supposed that "winter disappearance" is the main cause of mortality in this species (i.e. losses sustained during the period between egg laying and pupation; Varley *et al.*, 1974), host-plant-specific selection of sufficient strength acting at other stages in the life history could outweigh selection pressures due to intrinsic host-plant palatability or synchrony. If, for example, selection from palatability was higher against caterpillars on oak (as I found in my experiments, see Chapters 2 and 3) but pupal predation was considerably higher on all other host-plants, then we might still find caterpillar abundance highest on oak in the field—overall, it could still be the optimal host species. Such factors could certainly go some way to reconciling the discrepancy between winter moth performance I find on oak and its often comparative abundance on this host in the field (Shutt *et al.*, 2019a; Macphie *et al.*, 2020).

7.5. Future directions

In the context of this specific system there are several obvious lines of future enquiry. Cannibalism has been observed in a range of Lepidoptera and it may be a further buffering mechanism which exists in some species to allow them to cope with situations where resources are depleted, particularly as they approach the end of their developmental period (see Appendix 8). Experimental tests of the conditions under which cannibalism in spring-feeding caterpillars occurs could establish its significance as a potential buffering mechanism, and comparisons across temporal communities of caterpillars would be informative, as in the case of dietary breadth (see Chapter 2). My results have highlighted the potential importance for fitness of differences in palatability between individual trees (see Chapter 5). Future work should seek to further explore the significance of individual differences in host-plant quality and phenological development as a potential population-level buffering mechanism. Finally, to determine whether mismatch induced by climate warming is actually affecting spring-feeding caterpillar populations, we should seek to determine whether these species, relative to later-feeding species, are showing particular declines or range contractions.

More generally, the evidence I have presented here from the spring-feeding caterpillar guild should prompt us to critically re-examine systems in which we have previously assumed synchrony to be a significant factor. This could begin with the other levels in this system, and perhaps particularly the generally neglected primary producers. Experimentally, future work should determine the extent to which buffering mechanisms occur more widely, in other phenologically synchronised systems. With sufficient data it may be possible for us to go some way in evaluating the relative importance of different buffering mechanisms across taxa, and the extent to which these different mechanisms contribute to the dampening of the fitness effects of mismatch. Simple ecological factors, such as the degree to which passerines may be able to compensate for a lack of one food source by supplementing with another, or the relative nutritional value of different prey taxa as food, are still rather poorly understood. Since the climate is highly likely to continue changing over the coming years and decades, a shift is occurring among researchers towards an emphasis on how populations and communities might adapt and cope rather than simply quantifying potential negative effects (IPCC, 2022). When thinking about phenological synchrony and the MMH, the case of the winter moth and oak should strongly suggest to us that we rigorously test the criteria for the presence of mismatch in a system before assuming it (Samplonius *et al.*, 2020). Indeed, perhaps—methodologically, and as a field—we should even begin to assume buffering and an inherent robustness to change as the default in natural systems, until we can *demonstrate* otherwise.

7.6. Concluding remarks

The overarching question which I have sought to address here is, in a changing climate, does mismatch matter? The MMH was conceived as a very particular phenomenon, applicable and relevant to a certain specific set of circumstances. Insofar as I have argued here that synchrony is not as important as has been supposed—in the caterpillar system and perhaps beyond—it is because the criteria for mismatch have not been fulfilled to the extent which has hitherto been supposed: spring is a gradual, heterogeneous process, such that the resource peak caterpillars are exploiting is not so ephemeral; caterpillars possess a range of adaptations and buffering mechanisms which serve to ameliorate the effects of mismatch when it does occur. These buffering mechanisms do not invalidate the MMH, but caveat it.

An excessive focus on certain specific taxa in the tree/caterpillar/bird food-chain, as well as research centring on only a handful of study populations, has, I believe, presented a somewhat misleading picture of the significance of climate change on mismatch in these systems. Just as we see among spring-feeding caterpillars that the effects of mismatch are highly contingent on the particular species pairings of resource and consumer involved, so too in other study systems might an excessive focus on only a few taxonomic groups lead to a misleading impression of the operation of the MMH, and, by extension, the impacts of environmental change. Readers may have noted my rather cautious language throughout this discussion and indeed the thesis as a whole: the repeated use of ‘may’, ‘could’, ‘might’, and so on. I have tried at all points to emphasise the limited state of our knowledge in so many respects—that often we have only a very partial understanding of the ecology or life history of the species involved (e.g. the extent and significance of dietary generalism in caterpillars). We should be mindful of these limits on our knowledge and that ecosystems, communities, and even single species, are incredibly complex entities—we cannot hope to make reliable or robust predictions as to the effects of climate change on their populations by extrapolating from one or a few very specific instances.

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Appendix 1: Supplementary Information

Chapter 1

Table S1.1. Number of studies on the MMH dealing with different taxonomic groups. Data taken from Supplementary Materials in Samplonius *et al.* (2020).

Species	**No**	**Species**	**No**
Great tit	15	Black-headed grosbeak	1
Lepidoptera (caterpillars)	7	Black-throated gray warbler	1
Operophtera brumata	7	Black-throated green warbler	1
Pied flycatcher	6	Blue grosbeak	1
Tent Caterpillar	5	Blue -throated blue warbler	1
Blue tit	4	Blue-winged warbler	1
Caribou	4	Brewer's sparrow	1
Collared flycatcher	4	Canada goose	1
Cassin's auklet	3	Canada warbler	1
Daphnia	3	Carnivorous plankton	1
Oak processionary moth	3	*Carnus hemapterus*	1
Orange-tip	3	Cassin's vireo	1
Perch	3	Chestnut-sided warbler	1
Zooplankton	3	Coal tit	1
Apoidea	2	Colorado Potato Beetle	1
Broad-tailed Hummingbirds	2	*Cotesia bignellii*	1
Bumble bees	2	*Cotesia melitaearum*	1
Cod	2	Diving beetle	1
Cynipidae	2	Dolly Varden	1
Elk	2	Eastern whip-poor-will	1
Gypsy moth	2	Eastern wood peewee	1
Herring	2	Eurasian flower head weevil	1
Lepidoptera (adults)	2	Fish	1
Lesser Sandeel	2	Flies	1
Muskox	2	Golden Plover	1
Northern house wren	2	Gray catbird	1
Parasitoid wasp	2	Great crested flycatcher	1
Shag	2	Greater snow goose	1
Yellowtail flounder	2	Green-tailed towhee	1
Acadian flycatcher	1	Guillemot	1
Adelie penguin	1	Hammond's flycatcher	1
American dusky flycatcher	1	Hermit thrush	1
American redstart	1	Hermit warbler	1
Anthocharis cardamines	1	Hooded warbler	1
Aphid	1	Hoverflies	1

cont

Atlantic Mackerel	1
Autumnal moth	1
Black-and-white warbler	1
Lace bug	1
Lazuli bunting	1
Least flycatcher	1
Lepidoptera (adult)	1
Lesser snow geese	1
Light-bellied brent goose	1
Little auk	1
Louisiana waterthrush	1
Lymantria dispar multinucleopolyhedrovirus	1
MacGilliray's flycatcher	1
Magnolia warbler	1
Marbled white butterfly	1
Moth	1
Northern parula	1
Northern shrimp	1
Northern waterthrush	1
northern wheatear	1
Ovenbird	1
Pacific-slope flycatcher	1
Polar bear	1
Prairie warbler	1
Prothonotary warbler	1
Puffin	1
Razorbill	1
Red-eyed vireo	1
Rhinoceros auklet	1
Roe deer	1
Rose-breasted bunting	1
Ross's geese	1
Sand lance	1
Sanderling	1
Savannah sparrow	1
Scarce umber moth	1
Scarlet tanager	1
Sparrowhawk	1
Spizella	1
Spruce budworm	1
Storm petrel	1
Summer tanager	1
Swamp sparrow	1
threadfin shad	1
Townsend's warbler	1
Indigo bunting	1
tree swallow	1
Veery	1
Jumping plant lice	1
Kittiwake	1
Western cherry fruit fly	1
Western spruce budworm	1
Western tanager	1
Western wood peewee	1
Willow tit	1
Wood thrush	1
wood warbler	1
Worm-eating warbler	1
Yellow-billed cuckoo	1

Table S1.1 cont.

Table S1.2. Composition of the diet of tit (*Parus*) species in the Forest of Dean, Gloucestershire (Great Britain). Data taken from Betts (1955) . Percentages shown are of the overall diet of the individuals sampled from each species. Numbers of Lepidoptera consumed are sub-divided across developmental stages.

Month	Tit Species	Developmental Stage of Lepidoptera	% of Diet
Nov	great	adult	12
	blue	adult	0
	coal	adult	0
	marsh	adult	92
	great	pupae	6
	blue	pupae	23
	coal	pupae	5
	marsh	pupae	0
	great	larvae	14
	blue	larvae	17
	coal	larvae	13
	marsh	larvae	0
	great	egg	10
	blue	egg	0
	coal	egg	42
	marsh	egg	0
Dec	great	adult	52
	blue	adult	23
	coal	adult	24
	marsh	adult	35
	great	pupae	0
	blue	pupae	7
	coal	pupae	6
	marsh	pupae	0
	great	larvae	0
	blue	larvae	12
	coal	larvae	0
	marsh	larvae	0
	great	egg	26
	blue	egg	0
	coal	egg	0
	marsh	egg	0
Jan	great	adult	7
	blue	adult	0
	coal	adult	0
	marsh	adult	0
	great	pupae	0
	blue	pupae	0

cont.

	coal	pupae	0
	marsh	pupae	0
	great	larvae	0
	blue	larvae	24
	coal	larvae	0
	marsh	larvae	0
	great	egg	20
	blue	egg	0
	coal	egg	0
	marsh	egg	0
Feb	great	adult	0
	blue	adult	0
	coal	adult	0
	marsh	adult	9
	great	pupae	0
	blue	pupae	0
	coal	pupae	0
	marsh	pupae	0
	great	larvae	0
	blue	larvae	7
	coal	larvae	0
	marsh	larvae	12
	great	egg	0
	blue	egg	0
	coal	egg	0
	marsh	egg	0
Mar	great	adult	0
	blue	adult	0
	coal	adult	0
	marsh	adult	0
	great	pupae	0
	blue	pupae	0
	coal	pupae	0
	marsh	pupae	0
	great	larvae	7
	blue	larvae	17
	coal	larvae	10
	marsh	larvae	0
	great	egg	0
	blue	egg	0
	coal	egg	0
	marsh	egg	0
Apr	great	adult	0
	blue	adult	0
	coal	adult	0

cont.

	marsh	adult	0
	great	pupae	0
	blue	pupae	0
	coal	pupae	0
	marsh	pupae	0
	great	larvae	0
	blue	larvae	0
	coal	larvae	10
	marsh	larvae	0
	great	egg	0
	blue	egg	0
	coal	egg	0
	marsh	egg	0
May	great	adult	0
	blue	adult	0
	coal	adult	0
	marsh	adult	0
	great	pupae	0
	blue	pupae	20
	coal	pupae	0
	marsh	pupae	0
	great	larvae	84
	blue	larvae	56
	coal	larvae	0
	marsh	larvae	0
	great	egg	0
	blue	egg	0
	coal	egg	0
	marsh	egg	0
Jun	great	adult	0
	blue	adult	0
	coal	adult	0
	marsh	adult	0
	great	pupae	0
	blue	pupae	13
	coal	pupae	6
	marsh	pupae	13
	great	larvae	6
	blue	larvae	0
	coal	larvae	0
	marsh	larvae	0
	great	egg	0
	blue	egg	0
	coal	egg	0
	marsh	egg	0

cont.

Jul	great	adult	0
	blue	adult	0
	coal	adult	10
	marsh	adult	0
	great	pupae	0
	blue	pupae	0
	coal	pupae	0
	marsh	pupae	0
	great	larvae	0
	blue	larvae	0
	coal	larvae	0
	marsh	larvae	0
	great	egg	0
	blue	egg	0
	coal	egg	0
	marsh	egg	0
Aug	great	adult	6
	blue	adult	5
	coal	adult	0
	marsh	adult	5
	great	pupae	0
	blue	pupae	0
	coal	pupae	0
	marsh	pupae	0
	great	larvae	0
	blue	larvae	0
	coal	larvae	0
	marsh	larvae	21
	great	egg	0
	blue	egg	0
	coal	egg	0
	marsh	egg	0
Sep	great	adult	0
	blue	adult	0
	coal	adult	0
	marsh	adult	0
	great	pupae	0
	blue	pupae	0
	coal	pupae	0
	marsh	pupae	0
	great	larvae	24
	blue	larvae	19
	coal	larvae	22
	marsh	larvae	51
	great	egg	0

cont.

	blue	egg	0
	coal	egg	0
	marsh	egg	0
Oct	great	adult	0
	blue	adult	0
	coal	adult	0
	marsh	adult	0
	great	pupae	0
	blue	pupae	0
	coal	pupae	0
	marsh	pupae	0
	great	larvae	32
	blue	larvae	68
	coal	larvae	55
	marsh	larvae	9
	great	egg	8
	blue	egg	0
	coal	egg	0
	marsh	egg	0

Table S1.2 cont.

Chapter 2

Table S2.1. Establishment dates of caterpillar cultures on each host-plant species assayed in the experiment. The phenology of each host-plant species differed in the field. For each experiment "Time 0" was taken as the timing of the first recognisable leaf breaking (see Methods 2.3). The treatment groups for each host-plant species therefore began on different calendar dates, as indicated above. Variation in the calendar date timing of each treatment was minimised as far as possible, so as not to confound host-plant effects with any effect of hatch timing, but was limited based on the observed phenology of each species in the field. The latest treatments were begun several days after the earliest treatments.

Host-plant Species	**Date of Establishment**
Acer	1 May
Alnus	29 Apr
Betula	1 May
Crataegus	29 Apr
Malus	29 Apr
Prunus	29 Apr
S. alba	29 Apr
S. caprea	2 May
Quercus	4 May

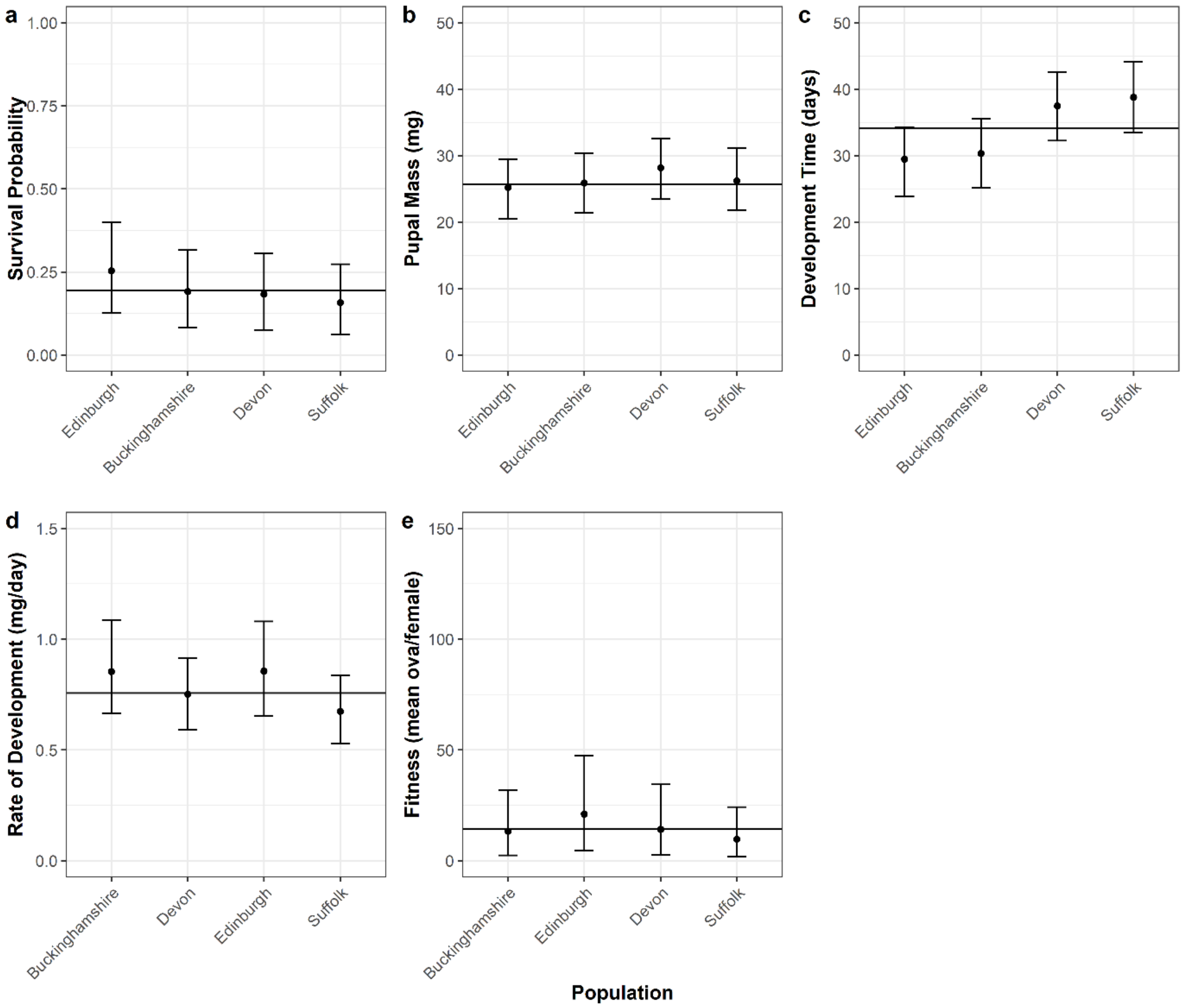

Figure S2.1. Overall winter moth performance in different populations across host-plants. Performance quantified as (a) survival probability, (b) pupal mass, (c) development time, (d) rate of development, and (e) estimated fitness. Mean estimates and 95% credible intervals shown. Global mean for each performance metric shown by solid line.

Table S2.2. Coefficients from the survival model which tests for differences across host-plant species, source population and any host by population interactions, indicative of divergence in survival among host-plants at different populations.

Survival Model	**Coefficient/Variance (Mean and CIs)**	**Effective Sample Size**
Fixed Terms		
Intercept	-2.296 (-3.351, -1.304)	10000
Random Terms		
Rearing culture	0.000473 (0, 0.00248)	1367
Population	0.04603 (0, 0.09103)	10000
Host-plant	2.096 (0.2705, 5.152)	9457
Population:Host-plant	0.8721 (0.3338, 1.507)	4341

Table S2.3. Coefficients from the pupal mass model which tests for differences across host-plant species, source population and any host by population interactions, indicative of divergence in mass among host-plants at different populations.

Mass Model	**Coefficient/Variance (Mean and CIs)**	**Effective Sample Size**
Fixed Terms		
Intercept	26.33 (19.57, 31.47)	10000
Random Terms		
Rearing culture	0.009934 (0, 0.03498)	9041
Population	0.6829 (0, 0.9573)	10000
Host-plant	33.35 (5.025, 79.51)	10000
Population:Host-plant	9.289 (3.708, 16.36)	2467
Sex	1695 (0, 77.49)	10000

Table S2.4. Coefficients from the development time model which tests for differences across host-plant species, source population and any host by population interactions, indicative of divergence in development time among host-plants at different populations.

Dev Time Model	**Coefficient/Variance (Mean and CIs)**	**Effective Sample Size**
Fixed Terms		
Intercept	33.94 (24.61, 42.27)	10000
Random Terms		
Rearing culture	0.007574 (0, 0.02736)	5620
Population	68.74 (1.433, 186.9)	1210
Host-plant	50.82 (10.19, 116.9)	10000
Population:Host-plant	8.624 (3.198, 15.08)	10000

Chapter 3

Table S3.1. Source populations of caterpillar livestock. The same populations were used across each year, though the number of females varies. Caterpillars from at least ten distinct broods were used in each case.

Species	Source Pop.	Year	Livestock (broods)	Max. Async. Tested	Async. Intervals (days)	Livestock/ Interval
winter moth *Operophtera brumata*	Edinburgh 55.9°N, -3.2°E	2019/20	126	19	2/3	20/30
		2020/21	84	65	5	20
mottled umber *Erannis defoliaria*	Edinburgh 55.9°N, -3.2°E and Callander, nr. Stirling 56.2°N, -4.2°E	2019/20	18	19	2/3	25/50
		2020/21	24	65	5	20
gypsy moth *Lymantria dispar*	Isle of Man 54.2°N, -4.5°E	2019/20	/			
		2020/21	25	65	5	20
black arches *Lymantria monacha*	Newcastle 55.0°N, -1.6°E	2019/20	/			
		2020/21	25	65	5	20
vapourer *Orgyia antiqua*	Edinburgh 55.9°N, -3.2°E	2019/20	30	58	20/28	50
		2020/21	45	65	5	20
scarce vapourer *Orgyia recens*	Bristol 51.4°N, -2.5°E	2019/20	/			
		2020/21	16	65	5	20

Table S3.2. Establishment dates of synchrony experiment on different host-plant species, across years. The phenology of each host-plant species differed in the field. For each experiment "Time 0" was taken as the timing of the first recognisable leaf breaking (see Section 3.3). The treatment groups for each host-plant species therefore begun on different calendar dates, as indicated above. Variation in the calendar date timing of each treatment was minimised as far as possible, but was limited based on the observed phenology of each species in the field. *Prunus* was featured in the experiment in 2020, but was excluded from further experiments and analysis due to poor larval performance and difficulty in obtaining foliage in the field.

	Year	
Host-plant Species	**2020**	**2021**
Acer	1 May	13 May
Alnus	29 Apr	15 May
Betula	1 May	12 May
Crataegus	29 Apr	5 May
Malus	29 Apr	12 May
Prunus	29 Apr	
S. alba	29 Apr	11 May
S. caprea	2 May	13 May
Quercus	4 May	16 May

Table S3.3. Coefficients from the survival model which tests for differences across host-plant species, source population and any host by population interactions, indicative of divergence in survival among host-plants at different populations.

Survival Model	**Coefficient/Variance (Mean and CIs)**	**Effective Sample Size**
Fixed Terms		
Intercept	-0.369009 (-1.990737, 1.291081)	10000
Day	-0.055704 (-0.083638, -0.030197)	8955
Year	0.965620 (0.424045, 1.580166)	8863
Day:Year	0.005014 (-0.006325, 0.017386)	8552
Random Terms		
Culture	0.007147 (0, 0.0267)	6502
Host:Intercept	1.4489085 (0, 4.1091113)	4004.3
Host:Day	0.0001262 (0, 0.0004221)	1557
Species:Intercept	2.4666591 (0, 7.487691)	3259
Species:Day	0.0008059 (0, 0.002444)	725
Host:Species:Intercept	1.527857 (0, 2.8114873)	1048
Host:Species:Day	0.000366 (0, 0.0006805)	1612
Year:Host:Species:Intercept	0.5968 (0, 1.2223424)	984
Year:Host:Species:Day	0.000068 (0, 0.0002549)	1012

Table S3.4. Coefficients from the pupal mass model which tests for differences across host-plant species, source population and any host by population interactions, indicative of divergence in mass attained among host-plants at different populations.

Mass Model	**Coefficient/Variance (Mean and CIs)**	**Effective Sample Size**
Fixed Terms		
Intercept	264.6904 (112.8519, 424.5265)	10165
Day	-0.5706 (-1.4005, 0.3208)	9907
Sex	-195.0917 (-399.4123, 7.8638)	10000
Year	22.6959 (11.6098, 33.0769)	10000
Day:Year	0.2312 (-0.1625, 0.6249)	10000
Day:Sex	0.1998 (-0.5785, 1.0309)	9643
Random Terms		
Culture	71.37 (33.53, 107.9)	10000
Host:Intercept	767.744 (0, 2478.9636)	3744
Host:Day	0.102 (0, 0.4097)	8075
Species:Intercept	4965.8513 (0, 20384.590)	4944
Species:Day	0.3441 (0, 1.283)	3325
Sex:Species:Intercept	15100.9526 (0, 0.00473)	1184
Sex:Species:Day	0.1911 (0, 0.6738)	4586
Sex:Host:Intercept	934.1316 (0, 2447.1267)	3615
Sex:Host:Day	0.1064 (0, 0.3816)	6700
Host:Species:Intercept	328.6811 (0, 1110.5065)	3293
Host:Species:Day	0.0890 (0, 0.3205)	6606
Sex:Species:Host:Intercept	3891.107 (2497.0981, 5467.852)	8102
Sex:Species:Host:Day	1.411 (0.8896, 1.968)	8645
Year:Host:Species:Intercept	176.8204 (42.97383, 353.4196)	9541
Year:Host:Species:Day	0.1531 (0.01585, 0.3461)	8373

Table S3.5. Coefficients from the development time model which tests for differences across host-plant species, source population and any host by population interactions, indicative of divergence in development among host-plants at different populations.

Dev. Time Model	**Coefficient/Variance (Mean and CIs)**	**Effective Sample Size**
Fixed Terms		
Intercept	36.168770 (26.354272, 45.950782)	10000
Day	0.064432 (-0.136809, 0.268996)	9043
Sex	-6.401142 (-15.250753, 1.766372)	10000
Year	-0.512803 (-1.995862, 0.978386)	9564
Day:Year	0.042057 (-0.009566, 0.088335)	7647
Day:Sex	-0.020965 (-0.104464, 0.071091)	10000
Random Terms		
Culture	1.696 (1.312, 2.077)	10430
Host:Intercept	5.721918 (0, 21.101781)	2364
Host:Day	0.001405 (0, 0.005287)	6558
Species:Intercept	89.51592 (0, 311.6431)	3567
Species:Day	0.05135 (0, 0.1551)	3410
Sex:Species:Intercept	26.636045 (0.00003, 94.99033)	5189
Sex:Species:Day	0.004678 (0, 0.01619)	2881
Sex:Host:Intercept	1.549449 (0, 5.530876)	4688
Sex:Host:Day	0.000416 (0, 0.001543)	8916
Host:Species:Intercept	15.619261 (2.404, 29.52100)	3412
Host:Species:Day	0.005338 (0, 0.01036)	3788
Sex:Species:Host:Intercept	9.116560 (4.776781, 14.235743)	6821
Sex:Species:Host:Day	0.002879 (0.000968, 0.004978)	8720
Year:Host:Species:Intercept	3.906120 (0.5345, 8.823590)	4030
Year:Host:Species:Day	0.002276 (0, 0.006107)	3348

Chapter 4

Table S4.1. Timing of bud collection in the field and the number of individuals sampled across host-plants. Buds were gathered across a period of several days to encompass the range of bud development stages.

Species	Dates Collected	No. Tree Individuals
alder *Alnus glutinosa*	23-28/4/2021	6
apple *Malus domestica*	23/4/2021	3
birch *Betula pendula*	27-30/4/2021	5
cherry *Prunus avium*	22/4/2021	4
hawthorn *Crataegus monogyna*	21-23/4/2021	6
oak *Quercus robur*	1/5/2021	3
sallow *Salix capraea*	24/4/2021	6
sycamore *Acer pseudoplatanus*	25-29/4/2021	6
willow *Salix alba*	25-26/4/2021	6

Table S4.2. Estimates of mean duration of survival when starved among caterpillar species and temperature treatments, with 95% credible intervals.

Species	Temp (°C)	Mean survival time (days, +95% CIs)
O. brumata	5	6.190357 (4.43443623, 7.913801)
	21	1.137793 (-0.62818129, 2.902768)
E. defoliaria	5	5.994565 (4.25043367, 7.772776)
	21	1.698595 (-0.06283889, 3.472769)
O. recens	5	14.794151 (13.05379555, 16.554478)
	21	5.502256 (3.78521068, 7.324867)
L. dispar	5	11.197075 (9.41737635, 12.994794)
	21	5.013417 (3.28607612, 6.755324)
L. monacha	5	27.598744 (25.80132154, 29.338913)
	21	6.110028 (4.33164355, 7.841192)

Table S4.3. Coefficients from the survival time model, which tested for differences in mean time to death when starved across treatment groups. Model was fitted without an intercept. The winter moth *Operophtera brumata* and the 5°C temperature treatment were treated as reference levels.

Overall survival time Model	Coefficient/Variance (Mean and CIs)	Effective Sample Size
Fixed Terms		
Speciesbrumata	6.1904 (4.4344, 7.9138)	10000
Speciesdefoliaria	5.9946 (4.2504, 7.7728)	10441
Speciesdispar	11.1971 (9.4174, 12.9948)	9683
Speciesmonacha	27.5987 (25.8013, 29.3389)	10000
Speciesrecens	14.7942 (13.0538, 16.5545)	10040
Temp21	-5.0526 (-7.5450, -2.5685)	10000
Speciesdefoliaria:temp21	0.7566 (-2.7782, 4.3691)	10490
Speciesdispar:temp21	-1.1311 (-4.7053, 2.3759)	10000
Speciesmonacha:temp21	-16.4362 (-20.0008, -12.8435)	10000
Speciesrecens:temp21	-4.2393 (-7.5993, -0.6847)	10000

Table S4.4. Coefficients from model testing for differences in the probability of survival across time. The winter moth *Operophtera brumata* and the 5°C temperature treatment were treated as reference levels.

Survival across time Model	Coefficient/Variance (Mean and CIs)	Effective Sample Size
Fixed Terms		
Intercept	97.6842 (73.6257, 123.3051)	984
Day	-14.8715 (-28.0710, -2.1408)	1214
Day^2	-0.7011 (-2.0812, 0.7771)	1002
Day:Speciesdefoliaria	2.0369 (-14.1850, 17.9638)	5000
Day:Speciesdispar	7.2666 (-4.8660, 22.6372)	3556
Day:Speciesmonacha	14.6849 (2.0911, 28.1155)	2894
Day:Speciesrecens	7.5609 (-4.8854, 19.8472)	3798
Day:Temp21	-67.5238 (-163.3906, 43.2627)	1743
Speciesdefoliaria:Day^2	-0.4462 (-2.7510, 1.7363)	3034
Speciesdispar:Day^2	0.4863 (-1.1389, 1.9894)	2078
Speciesmonacha:Day^2	0.5852 (-0.8714, 2.0063)	2166
Speciesrecens:Day^2	0.7178 (-0.6819, 2.1932)	2276
Temp21:Day^2	-63.2223 (-176.0114, 37.1714)	1245
Day:Speciesdefoliaria:Temp21	41.3199 (-64.9321, 148.4065)	4118
Day:Speciesdispar:Temp21	45.5455 (-69.7208, 147.0005)	2644
Day:Speciesmonacha:Temp21	53.3921 (-59.3051, 152.8432)	1570
Day:Speciesrecens:Temp21	50.8636 (-62.8314, 151.2210)	1704
Day:Speciesdefoliaria:Temp21:Day^2	29.8567 (-68.9189, 114.2378)	1693
Day:Speciesdispar:Temp21:Day^2	64.3368 (-36.1491, 178.0128)	715
Day:Speciesmonacha:Temp21:Day^2	62.6998 (-38.0017, 175.1035)	3087
Day:Speciesrecens:Temp21:Day^2	63.6395 (-36.4976, 176.5665)	4124
Random Terms		
Culture	0.03067 (0, 0.03765)	3556
Caterpillar Individual	2161 (1240, 3231)	5027

Table S4.5. Coefficients from bud utilisation model, which tested for differences in the ability of caterpillars to establish themselves living and feeding on unopened and opening buds of various stages. Model was fitted without an intercept. Response is probability of establishment by the end of a five day period after the start of the experiment.

Bud utilisation Model	**Coefficient/Variance (Mean and CIs)**	**Effective Sample Size**
Fixed Terms		
Bud Stage 1	-1.25893 (-2.33816, -0.27044)	10000
Bud Stage 2	0.05052 (-0.91096, 1.12394)	10000
Bud Stage 3	0.78944 (-0.27559, 1.75850)	10120
Bud Stage 4	0.92687 (-0.03740, 1.98598)	10000
Random Terms		
Culture	0.03712 (0, 0.1418)	9589
Host-plant	1.885 (0.3223, 4.522)	4287
Host-plant:Bud Stage	0.03833 (0, 0.1502)	10000

Chapter 5

Table S5.1. Coefficients from the model estimating overall probability of survival to pupation across treatment groups. Sycamore *Acer* and young foliage (“Age0”) treated as the reference levels.

Surv. time means Model	**Coefficient/Variance (Mean and CIs)**	**Effective Sample Size**
Fixed Terms		
Intercept	-864.856 (-1530.289, -311.667)	3897
Age13	-3.643 (-654.211, 612.901)	10000
hostBetula	626.490 (123.076, 1209.991)	5222
hostQuercus	363.871 (-116.923, 942.303)	7271
Age13:hostBetula	58.880 (-627.753, 771.382)	10000
Age13:hostQuercus	-66.312 (-773.864, 703.157)	10000

Table S5.2. Coefficients from the model estimating the time taken to pupation across treatment groups. Sycamore *Acer* and young foliage (“Age0”) treated as the reference levels.

Dev. time means Model	**Coefficient/Variance (Mean and CIs)**	**Effective Sample Size**
Fixed Terms		
Intercept	29.029 (22.328, 36.199)	9402
Age13	-4.002 (-14.008, 5.605)	10000
hostBetula	-1.797 (-9.025, 5.640)	9117
hostQuercus	-7.028 (-14.804, 0.598)	10000
Age13:hostBetula	6.383 (-3.623, 16.842)	9951
Age13:hostQuercus	4.324 (-7.153, 15.185)	10292

Table S5.3. Coefficients from the model estimating cumulative probability of survival to pupation across time among treatment groups. Sycamore *Acer* and young foliage (“Age0”) treated as the reference levels.

Surv. across Time Model	**Coefficient/Variance (Mean and CIs)**	**Effective Sample Size**
Fixed Terms		
Intercept	62.0965 (39.5711, 85.3403)	10512
Day	-5.6761 (-6.7065, -4.3699)	5802
Day:hostBetula	2.3421 (0.7552, 3.8419)	6169
Day:hostQuercus	1.0652 (-0.3659, 2.3988)	7083
Day:Age13	-0.7343 (-1.9141, 0.5529)	7551
Day:hostBetula:Age13	1.5186 (-0.3287, 3.4894)	7088
Day:hostQuercus:Age13	0.4893 (-1.2609, 2.3388)	7934
Random Terms		
Brood	213.9 (0, 736)	1841
Caterpillar Individual	3326 (1687, 5228)	3418
Host Tree Individual	98.89 (0, 337.5)	6013

Table S5.4. Coefficients from the model estimating cumulative growth across time among treatment groups. Sycamore *Acer* and young foliage (“Age0”) treated as the reference levels.

Area across time Model	**Coefficient/Variance (Mean and CIs)**	**Effective Sample Size**
Fixed Terms		
Intercept	-0.177605 (-1.153311, 0.788286)	10000
Day	0.422878 (0.059135, 0.770910)	10000
Day^2	0.028026 (0.009730, 0.046253)	10000
Day:hostBetula	-0.051975 (-0.524722, 0.410207)	10000
Day:hostQuercus	-0.445876 (-1.000358, 0.112911)	10000
Day:age13	-0.330319 (-0.913646, 0.219035)	10000
Day^2:hostBetula	0.038265 (0.012806, 0.064087)	10000
Day^2:hostQuercus	0.054902 (0.019735, 0.092142)	10000
Day^2:fage13	0.019265 (-0.012396, 0.052107)	10000
Day:hostBetula:fage13	0.176584 (-0.505028, 0.885597)	10000
Day:hostQuercus:fage13	0.796456 (-0.020789, 1.677369)	10000
Day^2:hostBetula:fage13	-0.044789 (-0.085018, -0.006943)	10000
Day^2:hostQuercus:fage13	-0.039342 (-0.092162, 0.014240)	9711
Random Terms		
Brood	213.9 (0, 736)	7808
Caterpillar Individual	3326 (1687, 5228)	10000
Host Tree Individual	98.89 (0, 337.5)	10411

Table S5.5. Coefficients from the linear model analysing the relationship between caterpillar dorsal view area and mass.

Area/Mass Model	**Coefficient (Mean and SE)**	***t* value**	***p*-value**
Fixed Terms			
Intercept	0.04847 (2.05660)	0.024	0.981
Area	1.33751 (0.08779)	15.235	0
R^2	0.595		
F	232.1, 1		
DF	156		

Table S5.6. Coefficients from the linear model analysing the relationship between caterpillar length and mass.

Length/Mass Model	**Coefficient (Mean and SE)**	***t* value**	***p*-value**
Fixed Terms			
Intercept	-20.030 (3.661)	-5.745	0
Length	4.030 (0.293)	13.755	0
R^2	0.545		
F	189.2, 1		
DF	156		

Table S5.7. Coefficients from the linear model analysing the relationship between caterpillar dorsal view area and length.

Area/Length Model	**Coefficient (Mean and SE)**	***t* value**	***p*-value**
Fixed Terms			
Intercept	2.710525 (0.078694)	34.44	0
Area	0.421082 (0.005909)	71.26	0
R^2	0.9102		
F	5078, 1		
DF	500		

Table S5.8. Coefficients from the linear model analysing the relationship between caterpillar dorsal view area and length, including a quadratic term to better fit the data.

Area/Length Quadratic Model	**Coefficient (Mean and SE)**	***t* value**	***p*-value**
Fixed Terms			
Intercept	1.9385619 (0.0539960)	35.90	0
Area	0.7356957 (0.0111687)	65.87	0
Area^2	-0.0088526 (0.0002979)	-29.71	0
R^2	0.9675		
F	7459,2		
DF	499		

Appendix 2: Pupal mass as a predictor of adult fecundity in the winter moth *Operophtera brumata*

Introduction

Pupal mass in insects can be a reliable predictor of adult female fecundity (Heisswolf *et al.*, 2009) and is therefore a very tractable measure of performance under different conditions—larger larvae produce larger pupae which yield larger females containing greater quantities of ova. Indeed, in the sizeable literature on the ecology and biology of the winter moth, variation in pupal mass across treatment groups is frequently interpreted as indicative of differences in fitness (see for example: Feeny, 1970; Wint, 1983; Kirsten and Topp, 1991; Tikkanen and Lyytikäinen-Saarenmaa, 2002; Belsing, 2015). In addition, if pupal mass falls below a certain level viability may be affected (Wint, 1983). Across insect species, the slope of the mass-egg relationship, the correlation coefficient, and the intercept can vary—and can be affected within a species by environmental conditions.

In analysing this relationship, it is possible that we might find these parameters differing, plastically or adaptively, within a species, under different conditions, to optimise fitness (for example, by producing more ova per unit mass on a given host-plant). Methodologically there is further a distinction to be drawn between potential fecundity (the number of mature oocytes or eggs in the reproductive tract) and realised fecundity (the number of fertile ova laid by a female during her lifetime)—the relationship between pupal mass and the latter is often far less precise (see for example Heisswolf *et al*., 2009). In the winter moth, only three studies have attempted to quantify the mass-fecundity relationship experimentally. Both Holliday (1977) and Rubtsov and Utkina (2011) trapped wild female moths in winter on tree trunks and measured their fresh mass and potential fecundity. The data obtained by the former are also reported by Singer and Parmesan (2010), though mistakenly attributed to a later paper (Holliday, 1985). Roland and Myers (1987) also trapped and weighed wild caught females, then back-calculated pupal mass, and estimated potential fecundity by dissection.

Here, I analysed the relationship between fecundity and pupal mass in the winter moth using my own data and that reported by the other studies described above. I tested if the relationship varied by population and if it was affected by the host-plant on which the caterpillar was reared. From this relationship I show how a metric of fitness can be estimated when caterpillar survival to pupation and pupal mass are both measured.

Pupal mass as a predictor of fecundity, and the effects of geographical and trophic factors

Methods

For the winter moth livestock reared in 2020 (Chapters 2 and 3), I measured the fresh mass of pupae raised in the captive rearing experiment one month after pupation (+/- 5 days). Pupae were then stored at 21°C until 1 September 2020, when they were placed outdoors in ambient temperature (Stirlingshire, UK; 56.069°N, -3.767°E) in sealed containers under an open canopy which provided shade. After female eclosion later in winter (December), they were killed in 75% ethanol and dissected. The potential fecundity of each individual was measured (no. oocytes/female). To analyse the mass-fecundity relationship in these data I fitted a general linear mixed effects model in the *R* v. 4.0.3 package MCMCglmm (Hadfield, 2010). To test for differences in the relationship between host-plants I included this as a random term. To account for potential between-population differences in the relationship this was also fitted in the model (Model 1. Response: Fecundity; Explanatory Fixed effects: Pupal Mass, Population; Random effect: Pupal Mass:Host-plant, with random slopes. Default priors, 500000 iterations with 250000 burn-in, thinning every 50 iterations). Due to the lower bound of pupal mass being approximately 10mg, it was mean-centred at 25mg.

In addition to my own data, I used the *R* package metaDigitise (Pick *et al.*, 2018) to extract the mass-fecundity data from the relevant figures in three previous papers which measured the fecundity and mass of winter moth individuals (Holliday, 1977; Roland and Myers, 1987; Rubtsov and Utkina, 2011). I combined these data with my own to generate an overall model and test for: (i) any differences in the mass-fecundity relationship between winter moth populations at different geographical sites; and, (ii) any significant difference in the mass-fecundity relationship between studies using adult female mass or pupal mass as proxies for fecundity (Model 2. Response: Fecundity; Explanatory Fixed effects: Pupal Mass, Dataset; Random effects: Host-plant. Default priors, 500000 iterations with 250000 burn-in, thinning every 50 iterations).

Results and discussion

Those studies which measure female mass, rather than pupal mass, unsurprisingly find that predicted fecundity at a mass of 25mg (the approx. mean pupal mass) is significantly higher (Holliday = 174.41 ova/female, CIs: 163.92, 184.67; Rubtsov and Utkina = 159.43, CIs: 154.18, 164.26 vs Roland and Myers = 140.23, CIs: 133.53, 164.26; Weir = 143.68, CIs: 139.24, 148.12) (Figure A1.1). This may be accounted for by individuals undergoing a loss of mass either during the period of development from summer to eclosion in winter (e.g. through water loss) or during the process of eclosion itself, which involves shedding the pupal case. As pupal/female mass increases in my data, fecundity increases significantly (slope = 9.81, CIs: 9.26, 10.34). This slope does not vary significantly relative to each of the other datasets (Holliday = 10.20, CIs: 9.46, 10.99; Roland and Myers = 9.57, CIs: 8.88, 10.25; Rubtsov and Utkina = 9.46, CIs: 9.04, 9.89).

Taking my own data separately, point estimates of the among host-plant species variance in the intercept (26.24, CIs: 0.00, 108.51; intercept mean-centred at 25mg) is greater than that of the slope (0.86, CIs: 0.00, 3.16) of the mass-fecundity relationship, but the lower bounds of the credible intervals approach zero suggesting these are non- or marginally significant. Pupal or adult female mass is therefore a consistent predictor of potential fecundity, with no significant geographical or host-specific variation across these data (Figure A1.1).

Estimating fitness in the winter moth

Factors such as survival, pupal mass, or development time are informative with regard to caterpillar performance on different host-plants, but are only a few of the many facets affecting overall fitness. Interpreting how these interact can be difficult: how does performance on a host species which yields high mortality but high pupal mass compare with one resulting in low mortality but low final pupal mass? Ideally, we could measure overall fitness in the field in each case, or as close an approximation to this as possible, to infer which is the optimal host-plant. Below I develop a metric of absolute fitness in the winter moth which I employ in Chapters 2 and 3.

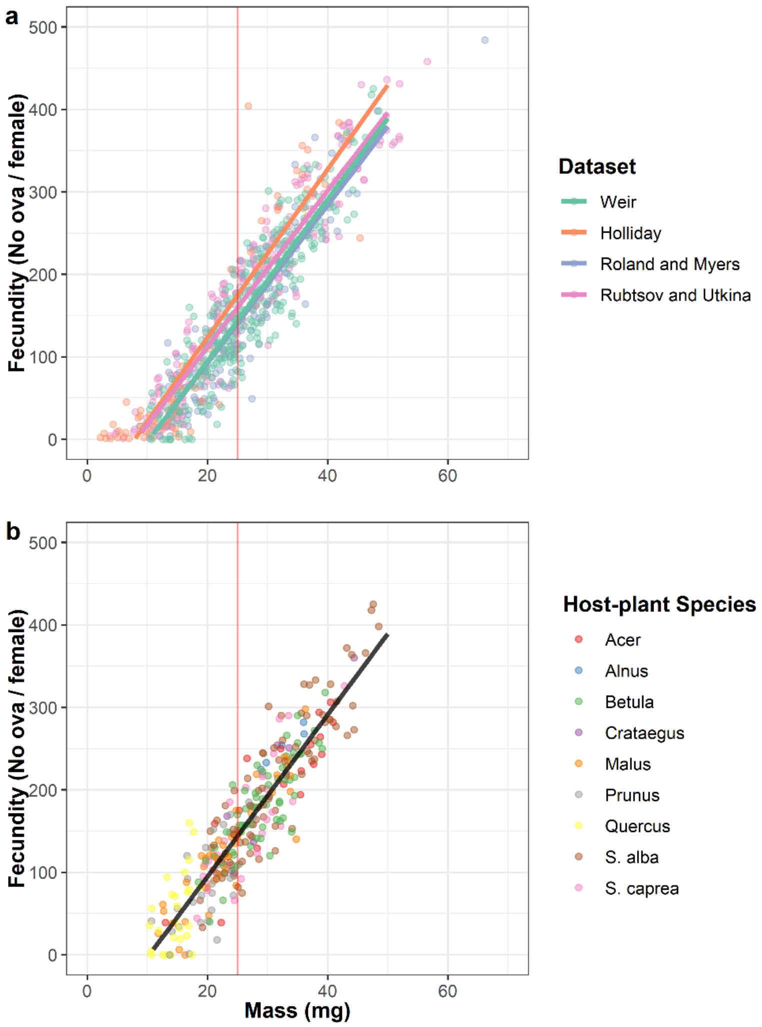

Figure A1.1. Relationship of winter moth pupal mass to potential female fecundity across (a) different studies and (b) across different host-plants in my own data. Regression line shows mean estimates for (a) each study (Slopes: Weir = 9.81, CIs: 9.26, 10.34; Holliday = 10.20, CIs: 9.46, 10.99; Roland and Myers = 9.57, CIs: 8.88, 10.25; Rubtsov and Utkina = 9.46, CIs: 9.04, 9.89) and (b) overall in the data from this study (slope = 9.81, CIs: 9.23, 10.32). Data in (a) were derived from Weir (this study), Holliday (1977), Roland and Myers (1987), and Rubtsov and Utkina (2011). Weir and Roland and Myers report fresh pupal mass, while Holliday and Rubtsov and Utinka use fresh female mass. Data in (b) were derived solely from the present study.

Assuming the pupal mass-fecundity relationship is linear, we can predict the fecundity of a moth—a more reliable signpost of fitness—from its pupal mass using the standard equation of a straight line:

$$y = mx + c$$

Thus:

$$\text{Fecundity} = m_{\text{mf}} * \text{Mass} + c_{\text{mf}}$$

Where m_{mf} is the posterior of the slope of pupal mass and potential fecundity found in my own data, Mass is the pupal mass in a given treatment group, and c_{mf} is the intercept of the mass-fecundity relationship. Using the posterior distributions of each of these terms from Bayesian models of my own data, it is possible to obtain a posterior for the predicted fecundity of an individual for a given pupal mass.

We can combine the predicted fecundity and the posterior of the probability of survival to give an estimate of fitness:

$$\text{Fitness} = \text{Fecundity} * \text{Probability of Survival}$$

Or, more completely:

$$\text{Fitness} = (m_{\mathrm{mf}} * \text{Mass} + c_{\mathrm{mf}}) * (\text{Survival})$$

This estimate of absolute fitness is therefore given as the *predicted ova per female in a given treatment group*.

This method is appropriate for categorical treatment groups, as in Chapter 2. In Chapter 3, I show that pupal mass and probability of survival vary with increasing asynchrony (a continuous variable) as well as across host-plant and caterpillar species (categorical variables). The performance/asynchrony relationship itself was fitted as a straight line in both mass and survival, which conformed well to the raw data:

$$\text{Survival} = m_{\mathrm{s}} * \text{Day} + c_{\mathrm{s}}$$

$$\text{Mass} = m_{\mathrm{m}} * \text{Day} + c_{\mathrm{m}}$$

Where m_{s} and m_{m} are the slopes of the change in probability of survival and pupal mass across time, respectively, and c_{s} and c_{m} are the intercepts. Thus, estimated fitness on any given Day in each of the different treatment groups, is given by:

$$\text{Fitness} = (m_{\mathrm{mf}} * (m_{\mathrm{m}} * \text{Day} + c_{\mathrm{m}}) + c_{\mathrm{mf}}) * (m_{\mathrm{s}} * \text{Day} + c_{\mathrm{s}})$$

Fitness here is therefore *the predicted ova per female on a given Day in a given host-plant treatment group*. From these posterior distributions it is possible to calculate a mean value and 95% HPD interval on estimated fitness.

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Appendix 3: A changing climate and its biological significance

Few natural environments, if any, are truly stable. Species exist within the context of continual flux in their abiotic and biotic conditions. These changes may be cyclical and periodic, directional, or stochastic; they may vary in their rate and magnitude; and may differ in terms of their spatial and temporal occurrence and scale. The corollary of these environmental changes is analogous variation in the selective pressures exerted by those conditions on organisms. Oscillations in an environmental variable around a mean, for example, can produce, through shifting selective pressures, an oscillation around a mean in a relevant phenotypic trait. Indeed, the climate is a very pertinent example of a suite of important environmental conditions which vary with space and time, which can change in consistent directions across the long- and short-term, but which also fluctuate stochastically and rhythmically, across the days and the seasons. Climate provides both a set of constraints and a set of resources to living things—levels of precipitation, humidity, and atmospheric CO_2, for example, affect growth in plants, while temperature directly affects the rate of biochemical reactions, and extremes can cause acute damage. Range sizes and limits are often dictated by the levels of climatic variables, such as rainfall and temperature. The extent of the fundamental niche of any given species, therefore, can be greatly influenced by climatic conditions.

Since the Earth's formation four and a half billion years ago, its climate has undergone dramatic changes. In the Phanerozoic Eon (541-0 mya) alone for instance—the period during which life has been a major feature of the planetary environment—estimates of global average temperature levels range from around 10°C to 36°C, compared with 15°C today (Royer *et al.*, 2004; Scotese *et al.*, 2021). Climate reconstructions of the Precambrian period (4600-541 mya) are less detailed and numerous, however it is generally accepted that the early Earth's atmosphere was likely anoxic, or almost so, with the main constituents, nitrogen and carbon dioxide, having been generated as the output of volcanism (Zahnle *et al*., 2010; though see for example Ohmoto *et al*., 2006). Higher levels of greenhouse gases such as carbon dioxide, alongside methane generated by early microbial life, might explain why, despite the output of the young sun being approximately 70% of modern levels, the Earth's temperature remained generally considerably higher than today during the early

Precambrian, perhaps as high as 50-70°C (Kasting and Ono, 2006; Doney and Schimel, 2007). Nonetheless, throughout the period, the otherwise hot conditions were punctuated by extreme cooling events, and spells of glaciation, perhaps on a planetary scale (the so-called "Snowball Earth"; Kirschvink, 1992). Part of the explanation for this dramatic variation could be that already high temperatures promoted high rates of CH_4 production in early methanogenic lifeforms. Methane may have reached atmospheric levels of 1000ppm, exceeding CO_2 concentrations (Kasting, 2005; Doney and Schimel, 2007). Where this ratio exceeds unity, models predict polymerised hydrocarbons forming such that the Earth would have been covered in a thin, organic haze—this would have served to re-radiate solar energy back into space, stabilising and then cooling the warming climate (Kasting, 2005).

From its earliest origins, then, life has both been shaped by climate and, along with geophysical forces, has contributed to driving changes in it—the two are tightly linked through complex interactions and feedback loops. Partly, this close association is due to the significance of carbon in living and climatic systems. As Doney and Schimel (2007) put it: "the Phanerozoic carbon cycle has shaped the environment and evolution of life while responding to the activity of living organisms and geological processes". The advent of photosynthetic organisms sometime in the middle of the Precambrian steadily increased the oxygen content of the atmosphere relative to CO_2, which likely contributed toward the general global cooling trend across this period to temperatures of 30°C by the end of the Proterozoic (the Eon in the Precambrian, 2500-541 mya) (Doney and Schimel, 2007; Scotese *et al.*, 2021). The oxygenation of the ocean and atmosphere, in turn, was critical in driving future evolutionary innovations, such as the eventual appearance of multicellularity (Canfield *et al.*, 2007). Across the Phanerozoic, temperatures fluctuated, following a roughly double humped pattern of higher levels in the early Palaeozoic and late Mesozoic (252-65 mya), and lower levels in the late Palaeozoic and late Caenozoic (65-0 mya) (Scotese *et al.*, 2021). Once again, both geological and biological forces had a role to play. In the late Devonian and Carboniferous periods, the large-scale expansion of plants on land increased oxygen levels in the atmosphere at the same time as removing large quantities of carbon dioxide, lowering radiative forcing and leading to glaciations (Lyons *et al.*, 2014). This certainly contributed to the first period of below average Phanerozoic temperatures.

Both the speed and the magnitude of environmental changes are significant in determining their biological impact. The eruptions of the Siberian Traps, a large volcanic province, at the end of the Permian (298-251 mya) released massive quantities of CO_2, almost doubling the atmospheric concertation (Taylor, 2004; Doney and Schimel, 2007). The resulting rapid rise in global temperatures due to the greenhouse effect, alongside ocean acidification, brought about the worst mass extinction in the Earth's history—some 90% of all known fossil species and 70% of known genera died out (Taylor, 2004). Similarly, the end of the Ordovician period (485-443 mya), marked by large-scale global cooling, expansion of the continental ice sheets, and lowering sea levels (Sheehan, 2003), resulted in the extinction of 83.5% of known genera (Christie *et al.*, 2013). Sudden, dramatic environmental changes are almost always, perhaps necessarily, associated with large-scale biological extinction. However, these can often be fairly taxon-specific—at the Palaeocene-Eocene Thermal Maximum, a sudden increase in temperature on the order of 5-6°C degrees which took place on a time scale of thousands of years, brought about extinctions in many marine groups, but mammals thrived (McInerney and Wing, 2011). Nonetheless, the role of rapid temperature changes, mediated via CO_2 levels and the greenhouse effect, seems increasingly supported as a driver of mass extinctions—most mass extinctions in the Earth's history correlate well with sudden changes in atmospheric CO_2 concentrations (Taylor, 2004).

Considering the panorama of the Earth's climate across the period during which life has been a major feature on the planet, we see considerable change, of varying magnitudes and speeds, during the most marked episodes of which species have died out on a tremendous scale (Taylor, 2004; Scotese *et al.*, 2021). Although there are varied causes of climatic changes, a major driver is thought to be the atmospheric concentration of greenhouse gases, particularly CO_2 (Doney and Schimel, 2007; IPCC, 2021). Levels of such gases are tightly associated with temperatures on a global and local scale (IPCC, 2021). In another example of living things influencing the climate, Man's activity, through the burning of various fossil fuels, is returning carbon to the atmosphere which was sequestered in the Carboniferous, prior to which temperatures were around 10°C higher than today (Royer *et al.*, 2004; Scotese *et al.*, 2021). Pre-industrial levels of CO_2 were among the lowest recorded throughout the Phanerozoic, and certainly on the lower extreme of the distribution (Royer *et al.*, 2004; Doney and Schimel, 2007). This has hitherto been mirrored by correspondingly low mean global temperatures, relative to the rest of the Eon—for the great majority of this time, for example, there have been no polar ice caps (Taylor, 2004). We live in the third great ice age (Taylor, 2004). But, with CO_2 outputs increasing post-industrialisation, levels are now higher than they have been at any point in the last two million years (Doney and Schimel, 2007; IPCC, 2021).

Today, once again, global temperatures are increasing. Both the speed and scale of these changes are unprecedented in thousands of years. Recent temperatures are at their highest in over 6500 years (throughout the present warm period, between glaciations), and have already risen by 1°C from pre-industrial levels (IPCC, 2021). Not only this, but the rate of this change is also considerable—since 1970, temperatures have increased at a greater rate than any other comparable period in the last 2000 years (IPCC, 2021). It is predicted that extreme weather events such as droughts, heatwaves, wildfires, heavy precipitation events, and tropical cyclones will occur more often in future, as a consequence of these climatic changes—the frequency and severity of which will depend on rates of continued anthropogenic outputs of greenhouse gases (IPCC, 2021). Estimates of future global temperature increases range from an additional 1-1.8°C by the end of the century with dramatically reduced emissions, to an increase of 3.3-5.7°C with increasing rates of emissions (IPCC, 2021). Considering the clear role that greenhouse gases have played as contributory, or even decisive, factors leading to historical mass extinctions, understanding the effects of present day anthropogenic emissions, their association with modern temperature changes, and the impacts of these climatic changes on species, and natural ecosystems as a whole, is a vitally important ongoing task for modern biology.

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Appendix 4: A history of the match-mismatch hypothesis and a critique of the literature

The idea of species being mistimed with respect to either the abiotic or biotic conditions of their environment, with negative consequences, is not a new one, and certainly pre-dates modern concerns about global climate change. However, surprisingly, the concept seems not to have been formalised as a systematic factor affecting individual fitness until the beginning of the twentieth century. The idea that variation in recruitment to populations of a species might be explicable in terms of the degree to which the phenology of their population matches that of an ephemeral resource originates in fisheries biology, and specifically in the work of Norwegian marine biologist Johan Hjort (1869-1948). In his classic work *Fluctuations in the Great Fisheries of Northern Europe* (Hjort, 1914) he considered the stages in the development of economically significant sea fish during which mortality within each species was most significant, with respect to determining overall future recruitment to the population:

> "We must […] look to the later stages of the eggs to find the conditions which determine the numbers of individuals in any year class[7]. This again leads us to the question, at which stage of development the most critical period is to be sought. Nothing is known with certainty as to this; such data as are available, however, appear to indicate the very earliest larval and young fry stages as most important." (p204)

Developing larval fish typically have an endogenous yolk supply, which they utilise while undergoing a transition to feeding on other food sources found in the environment (exogenous feeding). Hjort discussed the fact that when fish make this move from endogenous to exogenous modes of feeding there is often a clear decline evident in their populations:

> "It has long been a recognised fact, both in connection with artificial incubation of fish eggs and in the study of the youngest egg and larval stages in the sea, that the

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[7] "Year class" is a term used predominantly in fisheries biology, meaning the individuals added to a population in any given year, or the recruitment to that population.

> numbers of individuals rapidly decrease as soon as the newly escaped larvae have consumed their yolk and commence to seek food for themselves. All extant accounts of such experimental culture refer to this point, and anyone who has studied the earliest pelagic stages of the fish will know how difficult it may frequently be to find the young larvae in the same water where the eggs, a short time before, were abundant." (p204-205)

In connection with this idea, he noted the dramatic variability, often over a period of weeks, of the planktonic food of the young fish, as they transition from yolk-feeding to finding their own nourishment. From this, he reasoned:

> "It occurred to me therefore [that] if the time when the eggs of the fish are spawned, and the time of occurrence of this [planktonic] growth both be variable, it is hardly likely that both would always correspond in point of time and manner. It may well be imagined, for instance, that a certain—though possibly brief—lapse of time might occur between the period when the young larvae first require extraneous nourishment, and the period when such nourishment is first available. If so, it is highly probable that an enormous mortality would result. It would then also be easy to understand that even the richest spawning might yield but a poor amount of fish, while poorer spawning, taking place at a time more favourable in respect of the future nourishment of the young larvae, might often produce the richest year classes. In this connection it must be remembered that one single cod may spawn millions of eggs." (p205)

Hjort, then, in tying together the concepts of matching or missing the peak of food availability for these fish and subsequent changes in the recruitment to their populations, seems to have been the first to clearly state how phenological mistiming in one species, with respect to an ephemeral biotic resource—what is now referred to as 'phenological asynchrony'—could be detrimental to a population. It is important to note that, in this early literature on the effects of asynchrony in marine fish populations, it is the emphasis on *recruitment* to the population that is key. Hjort argued that the inherent variability in both the spawning date of the fish and the date of plankton blooms meant there was some built-in randomness in the system, in this trophic interaction between the fish and their food. This randomness, and consequent variation between years in the degree of match or mismatch between the timing of fish transitioning to exogenous feeding and the maximum availability of their food supply, explained the fluctuations in fish recruitment from year to year—perhaps even more importantly than the size of the spawning earlier in that season. Here we see the economic significance of Hjort's idea, and perhaps why it was first so explicitly articulated in this field. His original hypothesis in the specific context of fisheries is sometimes called the critical period hypothesis (Durant *et al.*, 2007; McCasker *et al.*, 2014), but the idea has come to be more widely known as the trophic mismatch hypothesis, the Cushing hypothesis (Kharouba and Wolkovich, 2020), or the match-mismatch hypothesis (or MMH, my preferred terminology, see Samplonius *et al*., 2020).

David Cushing (1920-2008), a British fisheries biologist, who introduced the term "match-mismatch" to the literature, was largely responsible for re-examining and re-appraising Hjort's ideas more recently, bringing the concept back to prominence and extending it in certain important respects. He proposed that temporal and regional variability in environmental conditions, which likely affect the development time of the fish from spawning (and at different stages in their life history, e.g. egg to larva, larva from endogenous to exogenous feeding) and the growth of plankton differently, meant that it was very difficult for the fish to accurately predict *when* to spawn. It would be difficult for them to estimate, based on environmental conditions, both how long their offspring would take to develop from spawning to exogenous feeding (which would preferably coincide with the peak of plankton production) and when the peak of plankton productivity was likely to be. This difficulty, he argued, meant that it was advantageous for the fish (in this case, herring), rather than adjusting their spawning date based on environmental cues, to instead spawn at a *fixed* time:

> "The correspondence between the herring 'races' and the production cycles suggests that the stock may depend for its survival for generations upon its relatively fixed spawning time related to a production cycle of a relatively constant character. It is the variability about its relative constancy that may generate part of the variability of year-class strength[8]. If this is true, the variability of year-class strength in the herring is associated with the density of food or of predators. At the same time it is generated within a comparatively short period, at the most up

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[8] "Year class strength", meaning the size of recruitment (the year class) to a population in any given year.

> till the time of metamorphosis, because the metamorphosed herring live close to the beaches, where the production cycle has quite a different character." (Cushing 1967; p207)

In later work, he elaborate upon this idea:

> "[I]f a fish population spawns at such a time that its larvae feed at the height of a production cycle, it is vulnerable to the variation of that cycle. Production cycles change with time in spread, amplitude, and timing. Climatic change is effective through changes in wind strength and direction, advancing or delaying the production cycles. Fish can only link their times of spawning to the production cycles in an indirect manner. If they spawn at a fixed season, the population has the best chance of profiting by the variability of the production cycle. If the spawning time varied randomly the link could not be sustained. So the fixity of spawning season really follows from the variability of the production cycle and the dependence of the fish populations upon it during their larval lives." (Cushing, 1969; p91)

Cushing therefore made his own unique refinement of Hjort's original hypothesis, and this is, strictly speaking, how he envisioned the "match-mismatch hypothesis" operating in nature (Cushing, 1990). Inter-annual fluctuations in fish recruitment are accounted for by the variation in peaks of plankton availability relative to the fixed developmental timeframe of the fish and, by extension, by the degree of match or mismatch between the maturing fish and their food supply.

Since then, however, the match-mismatch hypothesis has seen widespread application, well beyond the field of marine or fisheries biology (Durant *et al.*, 2007). In modern literature, the match-mismatch hypothesis is interpreted more generally and posits that phenological asynchrony (a difference in mean phenology) between a consumer and an ephemeral resource species results in negative fitness consequences for the consumer species, at the individual or population level (Samplonius *et al.*, 2020). Thus, the modern incarnation of the hypothesis has more akin to Hjort's original formulation than to Cushing's very specific idea. However, unlike Hjort, who focussed on recruitment to the population, modern authors include this as part of a wider consideration of how fitness in general is affected, at the individual and population level (Kharouba and Wolkovich, 2020; Samplonius *et al.*, 2020). The match-mismatch hypothesis is still typically applied in a trophic context, but has also been applied to mutualistic interactions (Iler *et al.*, 2013)—in each case, the logical is similar. Further, the hypothesis is usually conceptualised as a bottom-up trophic phenomenon, with species at higher levels attempting to match the phenology of prey species on which they depend at crucial periods in their life history. However, there is clearly the potential for top-down effects (Samplonius *et al.*, 2020), and there is a general failure to consider the natural corollary of detrimental effects on a consumer—such as a predator—which is the potential beneficial effects on the resource taxon of suffering reduced levels of predation (e.g. Deacy *et al.*, 2017). Migration, too, could result in its own form of the MMH—mistiming of departure in migrant species could lead to asynchrony with food resources or weather conditions at their destination, which could be driven or exacerbated by geographically heterogeneous climate change. For the purposes of simplicity, and due to the nature of my focus in the present work, I will use the terms consumer and resource for the remainder of this discussion, and will apply the hypothesis in a trophic context unless explicitly stated otherwise. The reader should, however, bear in mind the much wider applicability of these principles in a variety of other settings.

Even within the field of fisheries biology the match-mismatch hypothesis has remained a controversial idea (Durant *et al.*, 2007). As Cushing (1975, 1990) himself acknowledged, particularly in the marine ecosystems in which the idea was originally applied, it is difficult to test the hypothesis and to exclude alternative explanations for these patterns in the data. At a simple level, we can break the hypothesis down into two broad, testable components: firstly, that the resource in question shows some degree of ephemerality or seasonality in its availability; secondly, that fitness, recruitment, or some such measure of performance in the consumer taxon is dependent on the availability or abundance of that resource—in the degree to which they match the resource (Durant *et al.*, 2007; Kharouba and Wolkovich, 2020). These do not necessarily flow from one another: Durant *et al.* (2005) for example found that survival in Soay sheep lambs was not affected significantly by asynchrony between lambing and the peak of spring vegetation growth, on the Hebridean island of Hirta.

As will be evident from the discussion above, the MMH is in essence a very specific case of stabilising selection—it explains the adaptive, concurrent timing of a consumer with its resource. Where the availability of the resource shifts, selection exerted under the MMH can become directional, pushing consumer phenology in the same direction as that resource shift. Climate change, and warmer springs causing phenological advancement, is one such mechanism (see Chapter 1). Cushing (1969) himself recognised this idea very early, acknowledging that even though fish may spawn at a relatively fixed time, major shifts in the dates of peak plankton production would result in a slow adjustment of that spawning window, through shifting selective pressures:

> "The slow shift of time of peak capture of the Arctic cod suggests that a fish population can slowly adapt to climatic change. But on the scale of variability of the production cycle in timing it is a small-scale adaptation. The concept of the fixed spawning time linked to a variable production cycle opens the possibility of the changes in abundance with time. Stocks may increase dramatically or fail catastrophically, because the fixed spawning time keys in to the production cycle or misses it. Because populations do not easily become extinguished, a stock might survive at very low levels during a poor period, to recover later." (p91)

Samplonius *et al*. (2020) have pointed out that most work discussing phenological asynchrony and the MMH does so in the context of recent climate change, and attempts to interpret future ecological impacts in the light of our understanding of the operation of the MMH in these systems—in almost all cases, the evidence is entirely inadequate to do this. They define five criteria which must be tested and verified to clearly demonstrate that temperature change-induced phenological mismatch is occurring, in a trophic context:

> "Criterion 1. An ephemeral resource contributes a large proportion of the consumer's diet.
>
> Criterion 2. Asynchrony between consumer and resource phenology is increasing over time.
>
> Criterion 3. Variation in asynchrony is driven by inter-annual variation in temperature.
>
> Criterion 4. Asynchrony impacts negatively on consumer fitness.

> Criterion 5. Asynchrony impacts negatively on consumer population size, density or growth.” (p157).

Analysing 129 papers in a systematic literature review, Samplonius *et al*. (2020) found that only 2 studies addressed all five criteria, and 58% considered only two of them. The overwhelming majority of studies (97%) addressed Criterion 1—the dependence of the consumer species on an ephemeral resource—but 74% of these did so by a simple *a priori* statement or assertion that the resource was important and time limited. Criterion 2—that the asynchrony was increasing over time—was the next most tested criteria, with all the remaining trailing far behind. The fact that the majority of such studies relied simply on pre-existing natural history knowledge of the system in question, and did not explicitly test the *degree* or *extent* of the dependence of the consumer on the particular resource species (or guild) in question, highlights a wider failing in the literature to address the pre-existing, pre-climate change baseline of a given study system (Kharouba & Wolkovich, 2020; though see for example Singer & Parmesan, 2010).

Understanding this baseline of conditions is critical for determining the effects of climate change, though there is often little effort made to do so (Kharouba and Wolkovich, 2020). For example, in their review of 42 studies examining phenological mismatch, Kharouba & Wolkovich (2020) found that only 12 (29%) began before 1980 and, of those, only 2 had greater than three years of data. This means most studies in their dataset began *after* the most recent major increases in temperature due to climate change (IPCC, 2021), and are not long enough to establish a pre-climate change baseline on which to compare current levels of synchrony or asynchrony—they lack even enough data to infer a synchrony baseline from outlying years where mean conditions match those which are inferred for pre-climate change conditions. Aside from these primarily methodological points, it is widely assumed that perfect synchrony, achieved through stabilising selection due to the MMH, is the default expectation—there is seldom consideration given as to the extent to which *asynchrony*, and not synchrony, might be the default (or even adaptive) state in a given system (Singer and Parmesan, 2010; Visser *et al.*, 2012; see also Chapter 7).

Indeed, there are many deep problems with much of the literature on climate change and the MMH. This is not to undermine the quality or even the veracity of the results of the studies which have been carried out, but merely to emphasise that our understanding of this phenomenon in nature, let alone our ability to predict future changes, is still, excepting perhaps a few very well-studied species, in its infancy. There are, for example, inherent statistical difficulties in disentangling the direct negative effects of changes in the environmental conditions brought about by climate change, such as temperature, with those mediated through phenological changes in a resource (Kharouba and Wolkovich, 2020):s sudies wishing to demonstrate the MMH, must be able to separate the two (Criteria 4 and 5 in Samplonius *et al.*, 2020). In those studies where the fitness effects of asynchrony are measured, there is overwhelming bias towards measuring offspring fitness—where there is a clear, well-supported trend toward negative effects—with less focus on adults and populations (Samplonius *et al.*, 2020). In the latter two cases we lack clear evidence of any negative effects of climate induced asynchrony (Samplonius *et al.*, 2020). This is particularly significant in the case of populations, for if climate induced asynchrony does not impact population size, but simply reduces mean fitness overall, it may not have such an impact on wider communities (Criterion 5 in Samplonius *et al.*, 2020).

The current literature on climate change and the MMH also shows considerable geographical, taxonomic, and trophic/functional bias—there is a focus on secondary consumers, terrestrial systems, and to sites in Europe and North America (almost exclusively in the northern hemisphere) (Durant *et al.*, 2007; Visser *et al.*, 2012; Kharouba and Wolkovich, 2020; Samplonius *et al.*, 2020). We know, however, that the impact of climate on phenology can vary significantly across trophic levels (Thackeray *et al.*, 2016; Cohen *et al.*, 2018; Roslin *et al.*, 2021); that the ecological and trophic forces shaping marine and terrestrial food webs and regulating the populations of marine and terrestrial species are quite distinct (Kharouba and Wolkovich, 2020); and that the recent and ongoing changes in the climate are geographically heterogeneous across the globe (IPCC, 2021). Most aquatic based studies approach the MMH from the community or population perspective and consider the consumer and resource equally, while terrestrial systems focus predominantly on aspects of the individual life history and fitness of the consumer (Kharouba and Wolkovich, 2020). This is perhaps due to differences in the disciplines, but also the dynamics of interactions and feedbacks between trophic levels in these habitats—in aquatic systems, top-down dynamics tend to be more significant than in terrestrial systems. The timing of the resource peak in such systems can in fact be *determined* by the timing of any release from predation, or a reduction in the levels of predation (Kharouba and Wolkovich, 2020).

The idea that climate change is causing differential changes in the phenology of interacting species, such that many species, perhaps even whole ecosystems, are becoming mismatched, with potentially catastrophic effects, is compelling but is only patchily supported by the current evidence. A little considered fact, for example, is the extent to which the MMH is a very specialised phenomenon, affecting only a small number of taxa. Aspects of the life history and ecology of many species might render them more or less vulnerable to mismatch, varying across trophic levels, functional groups, and guilds. In contrast to nesting birds, for example, who rely on temporally narrow windows of food availability while rearing their offspring, reptiles are typically generalists, without reliance on an ephemeral food supply. In mammals, females accumulate food stores to help support the rearing of their offspring—in both instances, these taxa are rendered less vulnerable to climate-induced mismatch, precisely because their ecology is such that they are not as reliant on an ephemeral resource (Durant *et al.*, 2007) (see also Chapters 6 and 7). Those species or guilds which are affected, however, may still be key within an ecosystem (Varley *et al.*, 1974). Nonetheless, for such a widespread, widely cited hypothesis, there are serious deficiencies in the evidence underlying it (Kharouba and Wolkovich, 2020; Samplonius *et al.*, 2020). I would argue that, in the current state of the evidence, even qualitative, directional predictions as to the future effects of climate on species-pair systems, let alone ecosystems as a whole, must be highly caveated.

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Appendix 5: The host-plant and caterpillar phenological arms race

Caterpillars are not evolving in isolation. Undoubtedly, part of the reason that it is so difficult for them to match the phenology of their host-plants is that it is to the benefit of their hosts to avoid attack as much as possible. Indeed, spring-feeding caterpillars in particular seem to exert severe pressures of defoliation on trees, which can impact their future growth and development (Wesołowski and Rowiński, 2006; Rieske and Dillaway, 2008; Elkinton *et al.*, 2010). Caterpillars and their host-plants are involved in an arms race, of which the more obvious biochemical war—the development of noxious secondary chemicals, and counter-adaptation of physiological tolerance to them—is but a part. As in arms races between countries, where parties accumulate weapons of different kinds, this evolutionary conflict progresses on many fronts simultaneously. Far less obvious is the phenological competition which spring-feeding caterpillars and their hosts are engaged in, and which can very usefully be conceptualised as an arms race of its own.

As spring progresses and abiotic environmental conditions change, they will eventually pass a threshold beyond which growth becomes possible for deciduous trees (and, because of physiological variation, the precise nature of this threshold will likely differ between plant species). In order to maximise their growing season, it would be logical for plants to begin development as soon as conditions become conductive to growth. In the absence of all other pressures, we might expect selection to quickly set this as the default. In such a situation, however, it would be fairly easy for herbivorous insects wishing to exploit young, poorly-defended foliage, to follow the same environmental cues as those used by their hosts to time their development, and so to match their phenology. With herbivores precisely matching the phenology of their host-plant, any individual plants which start development *later* in the growing season would benefit from lower levels of insect-related herbivory damage, but at the cost of a truncation of their growing season—another clear example of the trade-offs operating in this system (see also Chapters 6 and 7). Between-individual variation in host-plant phenology, driven by diversifying selection exerted by spring-feeding herbivores, promotes, for example, bet-hedging strategies in those herbivores, leading to variation in their own phenology within broods and across the population, as well as physiological and behavioural buffering adaptations to ameliorate the effects of mismatch (see Chapter 6). The alternative approach would be conservative bet-hedging—consistently feeding later in the year though at the cost of increased investment in dealing with plant biochemical defences. In spring, then, the variation in host-plant phenology which results from the pressures of herbivory contributes to a depression of the fitness landscape for caterpillars, from a steep peak into a broad, flattened pulse (as in Figure 6.4) via portfolio effects. The variation, and tolerance of variation, built into this system has clear potential implications with regard to its robustness in the face of environmental perturbations, such as climate change.

The phenological arms race is, however, not equal. The *life-dinner principle* describes the inherent imbalance in the costs of failure in many biotic interactions, for example a predator-prey encounter, based on the notion that "[t]he rabbit runs faster than the fox, because the rabbit is running for his life while the fox is only running for his dinner" (Dawkins and Krebs, 1979). If the prey lose, they die and cannot reproduce. But, while paying a cost, predators can fail in many interactions with prey and still go on to reproduce. Due to asymmetry in the fitness costs of losing an interaction, one side in an ongoing arms race can therefore consistently "out-evolve" the other. As I have discussed in previous chapters, the consequences of mistiming for caterpillars can be severe, depending on the magnitude of that mistiming and the particular ecological interaction involved (see Chapters 3 and 4). And these costs are certainly greater than the costs experienced by the trees. Trees will suffer damage and reduced growth if caterpillars occur synchronously, and particularly if defoliation occurs at a large scale, but the rather delicate and immobile caterpillars will die if they find themselves without food. In this case, we therefore have an example of the life-dinner principle in reverse, where the consumer is under stronger selection than the resource. This, combined with the shorter generation time of these insects (annual versus several decades in their host trees), mean that they are likely to always be slightly ahead in this arms race, and perhaps more predisposed to persist in difficult and changing conditions. The sheer abundance of many of these spring-feeding caterpillar species in the field provides some indication of their success in overcoming the biochemical, structural, and phenological anti-herbivory strategies of their host-plants. Indeed, the fact that the "caterpillar peak" is often a distinct feature of spring only (see Chapter 1)—which is part of the reason for birds choosing to breed at this time—and that caterpillars are often more numerically abundant and biodiverse at this time than at any other throughout the year (Feeny, 1970) indicates strongly the extent to which the caterpillars have out-evolved their host-plants in this phenological niche. Using the arms race idea as a prism through which to view this system might also shed some light on the more unusual aspects of it, or the inconsistencies in our knowledge, and is a promising avenue for future work on the MMH in this system.

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Appendix 6: Table of terminology

Where I have used terms in the text that have a potentially ambiguous interpretation or where I have employed a specific definition that is not in widespread use, I give more complete definitions here.

Establishment

In Chapter 4, I define establishment as a neonate caterpillar beginning to feed and showing clear signs of growth in a particular host-plant treatment (including, for example, larger body size, green plant tissue visible inside body, and frass in and around where it is feeding).

Mistiming

As with *phenological asynchrony*. Generally used neutrally, not necessarily implying a negative fitness effect.

Palatability

Both the biochemical and biomechanical properties of plant material can affect its value as a food source for caterpillars, through variation in edibility, nutritional content, digestibility, and/or toxicity (see for example, Stamp & Casey, 1993). Here, I use palatability as a general umbrella term to cover all the ways in which consuming plants affects caterpillar fitness, which is what I am interested in here. For example, host *x* may be indigestible and host *y* may have high levels of noxious chemicals, but the palatability of both host-plants, and hence insect fitness or performance on them, could feasibly be equal.

Performance

Caterpillar fitness varies under different conditions, but cannot itself be easily measured. It is more likely that we will measure some component or contributory factor to fitness, such as survival, pupal mass (a proxy of fecundity), growth and development rates, etc. Here, I use performance as an umbrella term to include all of these various proxies of fitness. If, for example, performance is said to decrease over time, this implies that across various different metrics the individuals in question are affected negatively—e.g. decreased survival rates, decreased pupal mass, etc.

Phenological mismatch / trophic mismatch

Following Samplonius *et al*. (2020), I use this term specifically to describe cases where phenological events in the life history of two species occur asynchronously and *this negatively impacts the fitness of the consumer/dependent taxa*. *Phenological* mismatch refers to negative effects arising out of the general mistiming of phenological events. *Trophic* mismatch specifically refers to synchronised trophic interactions.

Phenological niche

The temporal window during which a species occurs, where this is specific and well-defined. The classic phenological niche of spring-feeding caterpillars is a finite period immediately following bud-burst on their host trees.

Phenological sensitivity to temperature

The extent to which a species changes its phenology for a given unit change in temperature conditions, ie. the slope of the plastic response of phenology against temperature.

Phenological synchrony

I use this as a neutral term to indicate that phenological events in the life history of two species occur contemporaneously, as in Samplonius *et al.* (2020). Use of asynchrony to describe these events being temporally misaligned does *not necessarily* imply any fitness consequences, though does not preclude it.

Appendix 7: Host-plant and moth species studied

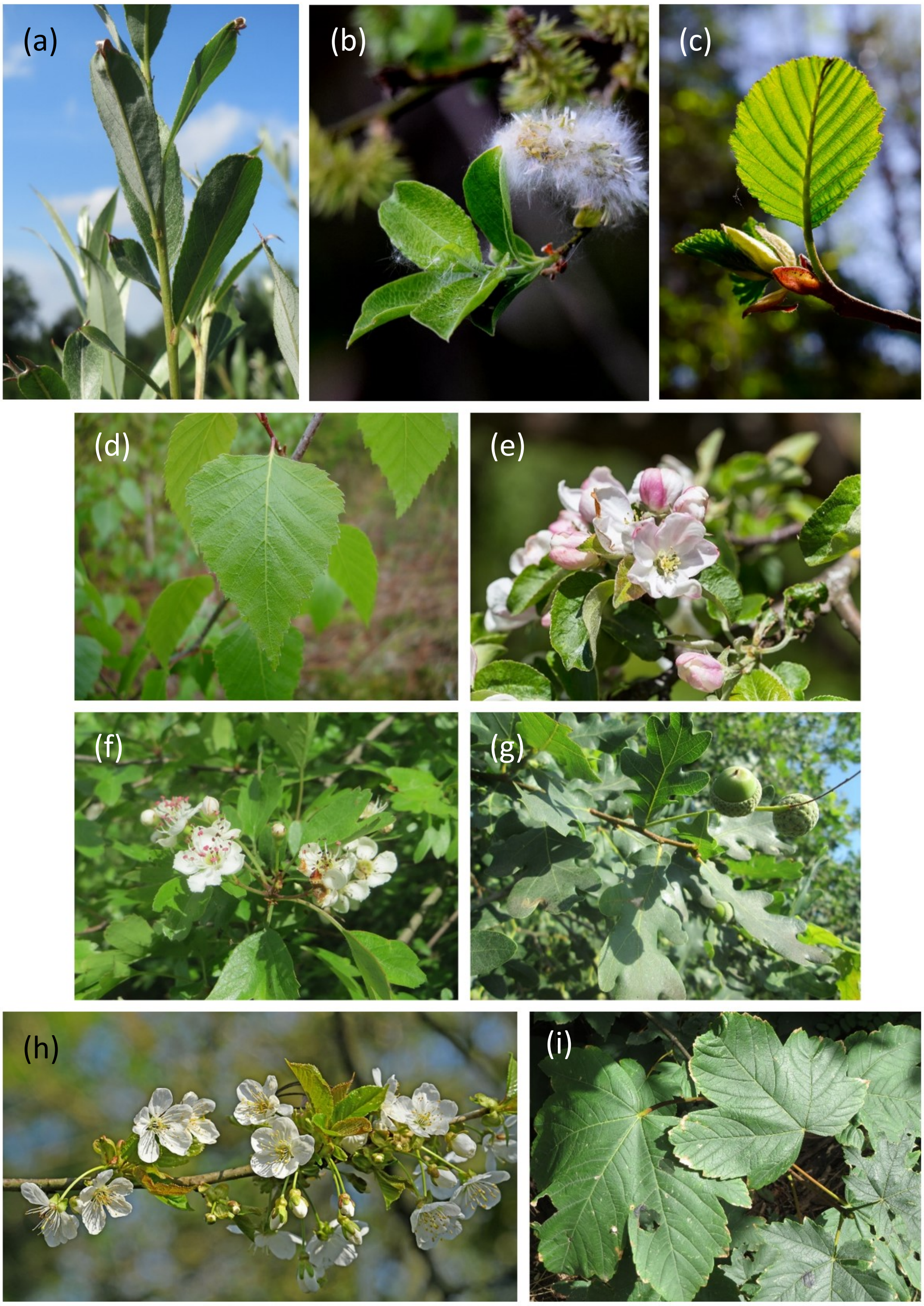

Figure A7.1. Host-plant species studied in the experiments described in this thesis. (a) Willow *Salix alba*, (b) Sallow *Salix caprea*, (c) Alder *Alnus glutinosa*, (d) Birch *Betula pendula*, (e) Apple Malus domestica, (f) Hawthorn *Crataegus monogyna*, (g) Oak *Quercus robur*, (h) Cherry *Prunus avium*, (i) Sycamore *Acer pseudoplatanus*. Image credits: Andreas Rockstein (a, f, g, I), Giuseppe Morlando (b), Tero Laakso (c), dragonfly201011 (d), Mariya Novikova (e), Karin Rogmann (h). From Flickr.org, reproduced under a creative commons licence.

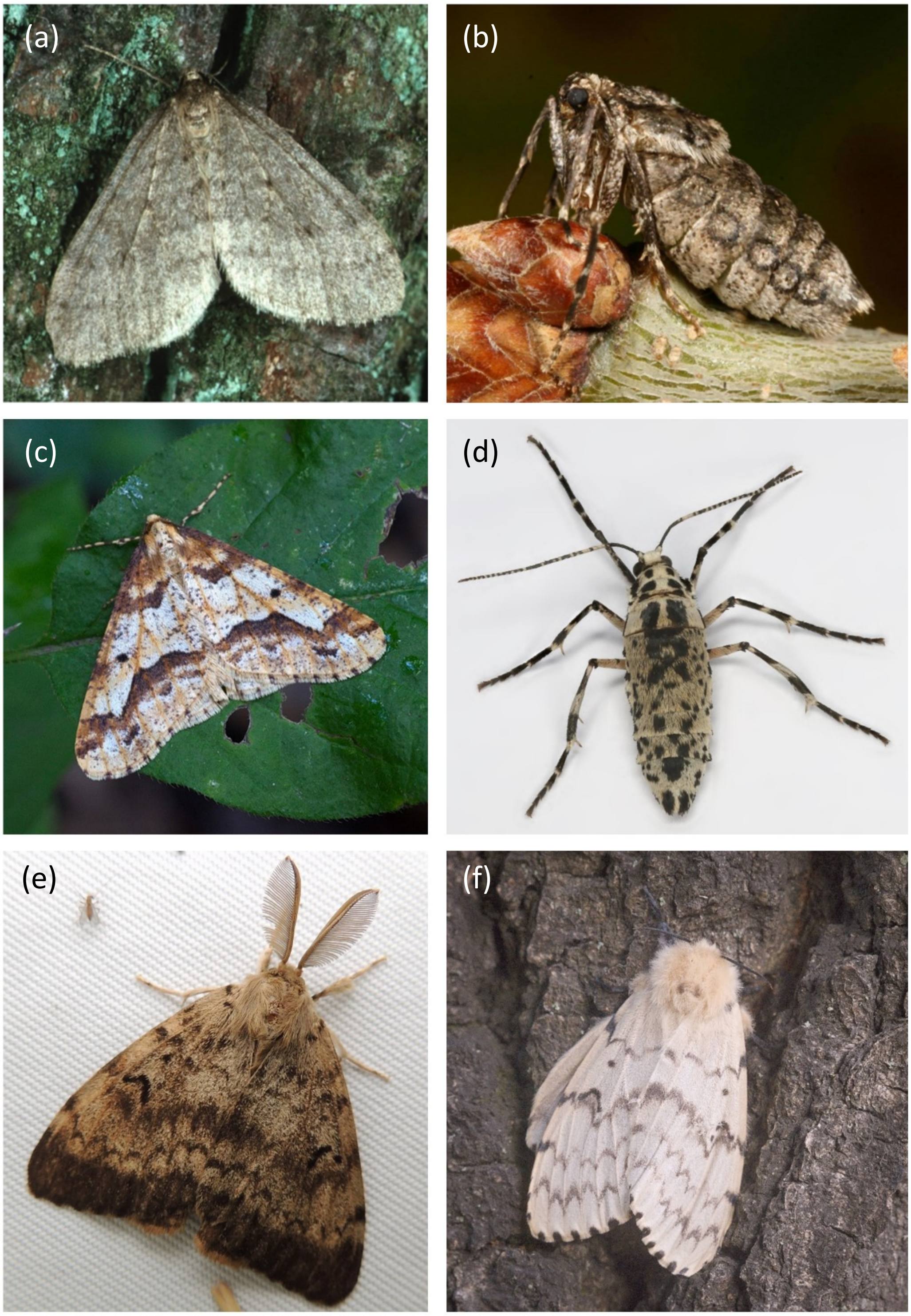

Figure A7.2. Adults moths of the caterpillar species featuring in the experiments described in this thesis. Winter moth *Operophtera brumata* (a) male and (b) female. Mottled umber *Erannis defoliaria* (c) male and (d) female; Gypsy moth *Lymantria dispar* (e) male and (f) female. Image credits: Louis-Michel Nageleisen (a), Gyorgy Csoka (b), Urmas Ojango (c), Janet Graham (d); Anita Gould (e), Hedera.Baltica (f). From Flickr.org and ForestPests.org, reproduced under a creative commons licence.

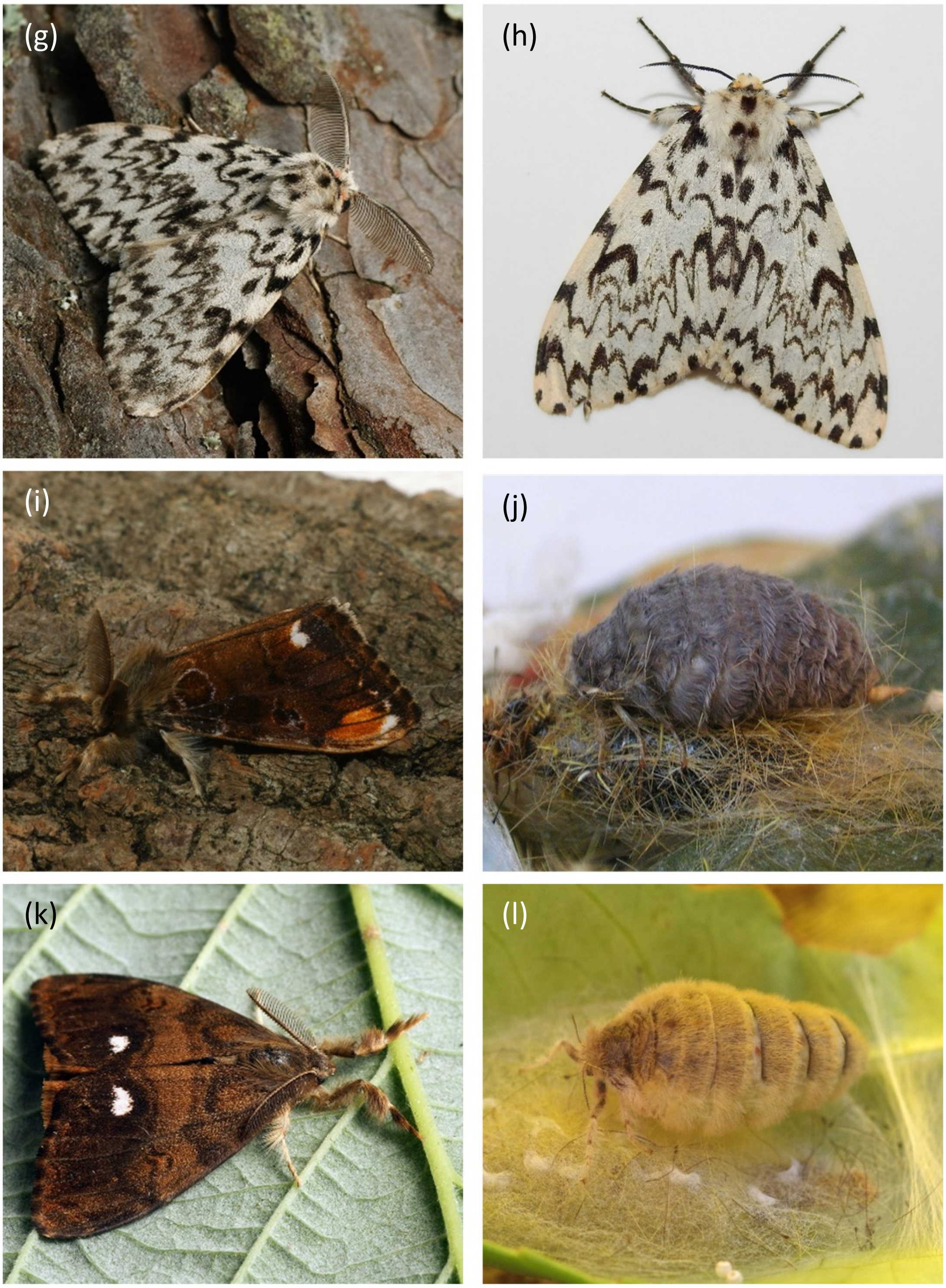

Figure A7.2 *cont*. Adults moths of the caterpillar species featuring in the experiments described in this thesis. Black Arches *Lymantria monacha* (g) male and (h) female. Scarce Vapourer *Orgyia recens* (i) male and (j) female. Vapourer moth *Orgyia antiqua* (k) male and (l) female. Image credits: Ilia Ustyantsev (g), Nick Dobbs (h), Ilia Ustyantsev (i), Ben Smart (j), Ilia Ustyantsev (k), Will George (l). From Flickr.org, reproduced under a creative commons licence.

Appendix 8: Cannibalism observed in captive winter moth caterpillars *Operophtera brumata*

Although almost all Lepidoptera are exclusively phytophagous, predatory behaviour, including cannibalism, has been observed in many species (Pierce, 1995). Extreme polyphagy, such as we see in many spring-feeding caterpillar species, is frequently correlated with a propensity to cannibalism (Richardson *et al.*, 2010). Omnivory on poor quality diets can improve performance (LoPresti, 2018), which may explain the evolution of this behaviour in some instances. Cannibalism in Lepidoptera can be size-dependent, with larger individuals selectively targeting smaller caterpillars of earlier instars (Semlitsch and West, 1988). In Britain, the orange tip butterfly *Anthocharis cardamines* and dun-bar moth *Cosmia trapezina* are two species known to exhibit this behaviour as caterpillars (Ford, 1945; Maitland Emmet and Heath, 1992; Skinner, 2009; Waring *et al.*, 2017). However, to my knowledge, it has not previously been reported in the winter moth.

I observed cannibalism in winter moth caterpillars on three occasions in 2020 and twice in 2021, while performing upkeep on the rearing cultures. It may have occurred more often but escaped my notice. In almost all of these instances, caterpillars were observed to begin feeding on another individual which was in the process of moulting (Figure A8.1a). Caterpillars were always provided with an excess of food in the rearing cultures, and it seems unlikely therefore that they were driven to this behaviour through starvation. In one notable instance a group of three different caterpillars began feeding on the same moulting caterpillar (Figure A8.1b), which was unable to move or flee. As well as strict cannibalism, I would frequently observe caterpillars ‘pinching’ one another, especially when in their final instars. The attacking individual would not begin feeding on the other individual—the attacked individual would usually thrash its head from side to side, which typically caused the attacker to move off.

Winter moth caterpillars undergo occasional years of extreme abundance, which can result in trees becoming entirely defoliated (Feeny, 1970). The caterpillars are able to feed on various low growing, ground-cover plants, like bilberry *Vaccinium* and heather *Calluna* (Porter, 2010; Robinson *et al.*, 2010; Henwood *et al.*, 2020), and in years where trees are

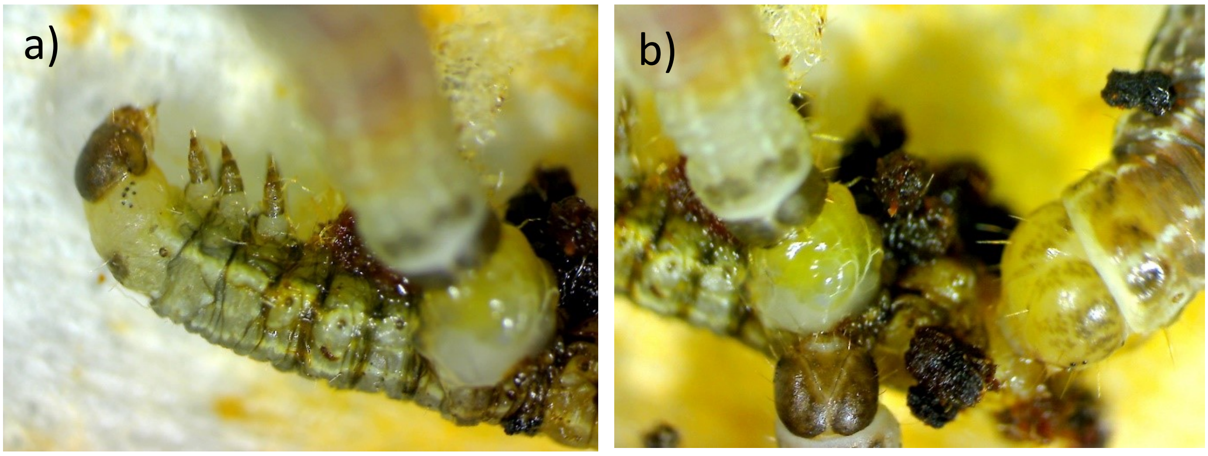

Figure A8.1. Cannibalism in the winter moth *Operophtera brumata*. Caterpillars typically predated individuals which were in the process of moulting (a) and therefore unable to flee or resist. Several caterpillars, shown here, were observed feeding collectively on the same moulting individual (b). They have eaten through the side of the prey individual's cuticle, spilling the contents of its body cavity.

defoliated and intraspecific competition is great, late instar individuals may descend from trees and complete their development on these alternative host-plants (Henwood, 1989). In a similar fashion, cannibalism may help individuals complete the final stages of their development when under stressful conditions or in particularly high density populations. Cannibalism among Lepidoptera may be more common than previously realised as it is not unusual, when breeding species in captivity, for individuals within a culture to 'go missing', with no apparent explanation.

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Appendix 9: A new trap design for the flightless females of winter-active moths

Adult winter moths *Operophtera brumata* eclose during the coldest months of the year, late November to early January in Britain (Briggs, 1957; Maitland Emmet and Heath, 1992; Skinner, 2009; Waring *et al*., 2017). Females are brachypterous and incapable of flight (Skinner, 2009). After emerging from their pupa they ascend the trunk of a nearby tree (Connell, 2013), mating *en route*, and lay their eggs on the bark, branches, and buds. The fact that these species are flightless makes collecting specimens of the adults difficult. Light trapping is effective only for the winged males (Briggs, 1957), and sugaring (Dickson, 1976; May, 2014) cannot be employed because they lack functional mouthparts. However, to conduct the experiments described here, I required adult females to provide ova for laboratory livestock. Previous authors have employed various techniques of intercepting females as they ascend trees or posts. Banding involves painting a sticky substance around the circumference of a trunk in order to trap the insects (Briggs, 1957; Holliday, 1977; Kimberling *et al*., 1986; Hibbard *et al*., 2010). This is used frequently in agricultural situations, where the goal is to prevent the moths reaching the canopy and laying their eggs there, but it often kills them. To collect adults without damage, others have used 'lobster-pot' style trunk traps which funnel individuals away as they climb (Varley *et al*., 1974; Holliday, 1977; Buse and Good, 1996). These traps, however, are usually large, conspicuous, fragile, and tend to be difficult to install and remove (Briggs, 1957; Embree, 1965; Schneider, 1980). Furthermore, they are generally quite substantial constructions which require a large quantity of materials and time to build.

For my experiments, I wanted a quick, cheap, and easily assembled line of traps that could be deployed, moved, and removed without much effort, and which would also collect large numbers of individuals for breeding in the lab. I developed a trap using 500ml plastic bottles with the top end cut off and inverted to create a lobster-pot type body (Figure A9.1). A tube of nylon stocking was fed through the mouth of the bottle and secured inside the trap. A band of webbing was fixed to the outside body of the bottle trap. These trap units were then fixed to tree trunks, with the nylon stocking tube pinned open and facing downwards. The tube of

Figure A9.1. Trunk traps for female winter moths *Operophtera brumata*. Traps comprise a 500ml plastic bottle with the top removed and inverted to create a 'lobster-pot'. A tube of nylon stocking is secured inside. The trap is fixed to the tree trunk via webbing, and the nylon tube extended and pinned open on the trunk. This funnels the females ascending the trunk into the trap body (c-d), where they remain. Visible in (d) is a gynandromorphic female, highlighted by the arrow.

Figure A9.2. Winter moth trunk traps in operation at (a) Glen Finglas, Callander, Stirlingshire (UK), on young oak trees *Quercus robur*, and (b) the Hermitage of Braid LNR, Edinburgh (UK), on a mature sycamore *Acer pseudoplatanus*. To maximise the number of individuals collected, I typically deployed several traps per tree, to cover around a third of the trunk circumference.

nylon acted to direct individual moths ascending the trunk upwards and into the body of the bottle trap. Once inside, they seemed unable to escape (Figure A9.1c-d). This design was developed and improved over several winters (2018-2021), and has been consistently employed with much success. Traps were typically deployed several to a tree and checked at weekly intervals (Figure A9.2). Adult females could then be taken to the lab and provided with laying media. I found that in the correct location, several dozen traps could collect consistently over a hundred females in a period of one to two months.

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Appendix 10: Factors affecting local adaptation and host race formation in spring-feeding caterpillar species

One way in which spring-feeding caterpillars could minimise mismatch in a complex, heterogeneous woodland environment is by adapting to the phenology of locally prevalent host-plant species, or perhaps even individual host-plants. In Chapter 2, I found evidence of geographical divergence in winter moth performance on different host-plant species across Britain, but these patterns did not seem to reflect the flora at a very local level (e.g. < 1km; compare Chapter 2, Table 2.3 with Figure 2.4). In other populations of the winter moth we can see a clearer signal of adaptation—in parts of Scandinavia, for example, performance can be locally higher on *Betula* and *Prunus* in areas where these species are very abundant (Tikkanen *et al.*, 1998, 1999; Belsing, 2015). Similarly, in the Scottish Highlands and in the Orkney islands, where trees are less frequent, we can see a marked specialisation on heather (Kerslake *et al*., 1996, 1998; Kerslake and Hartley, 1997). This suggests that adaptation in this species may occur, but only at fairly large spatial scales in peripatric populations, or under unusual conditions, such as in radically distinct habitats like heathlands or islands where populations are more isolated.

Considering that, compared to the other species studied here (see Chapter 3), mismatch exerts relatively strong fitness effects in the winter moth, it is interesting that this species does not show clearer adaptation at a smaller spatial scale, which might serve to buffer local asynchrony. Two other spring-feeding caterpillar species represent interesting and illuminating points of comparison: the larch tortrix moth *Zeiraphera griseana* (syn. *Z. diniana*; Agassiz *et al*., 2013) and the fall cankerworm *Alsophila pometaria*.

The larch tortrix moth flies in midsummer (both males and females are fully winged), and the caterpillars feed on larch and other conifers, spinning a hollow tube together among the needles within which to feed (Maitland Emmet and Heath, 1992). Like the winter moth it is a periodically out-breaking pest species—populations peak every 8-10 years in the Swiss Alps (Emelianov *et al*., 1995). Within woodlands, populations sourced from stands dominated by either *Larix* or *Picea* species show marked differentiation in survival across host-plants, and their spring hatching phenology closely matches the timing and rate of development of their particular host-plant (Emelianov *et al*., 1995). This high degree of specialisation has arisen in this species apparently sympatrically, since there are no rigid spatial or temporal barriers between different micro-habitats (individuals of each host-plant species) preventing reproduction of individuals which developed in each environment (Jiggins *et al*., 2005). However, adult moths of both sexes show a preference for alighting on the branches of the tree species on which they developed—as females call, releasing pheromones to attract mates, these two factors will compound and tend to cause assortative mating (Emelianov *et al.*, 2001, 2003). This is itself exaggerated by forest structure: even clumping of similar host-plant species at a very small scale can facilitate divergence in other traits (e.g. calling pheromones), leading to further host-plant specialisation. In the field there is still a degree of hybridisation between the different host races that have arisen in the larch tortrix, but this is not sufficient to break down the divergence (Emelianov *et al*., 2004; reviewed in Jiggins *et al*., 2005).

In the fall cankerworm, like the winter moth, the adult females are incapable of flight and the caterpillars are highly polyphagous, feeding on a range of deciduous trees (Mitter *et al*., 1979). But it is distinct in that its populations contain both sexually and asexually reproducing individuals (Mitter *et al*., 1979). Douglas Futuyma and his colleagues studied the species intensively in the latter part of the last century at populations in Long Island, New York (Mitter and Futuyma, 1979; Mitter *et al*., 1979; Futuyma and Philippi, 1987). Here, they found that ~13% of the population comprised males and sexual females, while the remaining individuals were asexual (Futuyma and Philippi, 1987). Mating is required for egg-laying, but the contribution of paternal genes to the offspring of asexuals is minimal, and often non-existent (Mitter *et al.*, 1979). There is, however, definite introgression of genes from the sexual part of the population into the asexuals at a very low level. They found that the prevailing asexual genotype could differ across extremely short distances (several hundred metres), rapidly shifting in prevalence among different woodland habitat types, such as clumps and stands of predominantly one host-plant species (Mitter *et al*., 1979). The fact that the fall cankerworm is capable of asexual reproduction, therefore, seems to allow for adaptation to host-plants that are abundant at an extremely local level—the sexual individuals exist at a low background frequency throughout habitat types and provide a pool of genetic diversity and variation from which the asexual phenotypes rapidly rise to predominance, depending on the particular habitat patch (Futuyma and Philippi, 1987). Such high levels of spatially local adaptation would perhaps not be possible in a sexually reproducing species (Mitter and Futuyma, 1979).

These two species, sharing many of the ecological traits typical of spring-feeding caterpillars, increase their mean fitness by adapting to flora at a very local level. Why do we not see adaptation at the same scale in the winter moth, or, indeed, many other spring-feeding species? We can see from the case of the fall cankerworm that although host-plant species can exert substantial selective pressures, promoting phenotypic divergence, this is likely to be dampened by recombination. In order to achieve divergence at such a small spatial scale—in both winged species, and those with apterous females—substantial barriers to gene flow much exist. In the fall cankerworm, widespread asexuality prevents the dilution of an optimal genotype in a given habitat type; in the larch tortrix, the spatial structure of the habitat, amplified by individual host-plant preference, dampens out mixing, and enables specialisation. Aside from the flightlessness of females, there are no obvious mechanisms in the winter moth by which this could take place. One might argue that, as in the larch tortrix, habitat structure and individual choice, perhaps in the males, might result in a similar outcome, but the larch tortrix has a far more restricted diet than the winter moth (Maitland Emmet and Heath, 1992). It occurs in coniferous woodlands, which typically have lower floral biodiversity than deciduous woodlands, and essentially feeds on only two species. Its fitness landscape is therefore rather bimodal. In the winter moth, the sheer breadth of the diet likely acts against divergence through trade-offs in the various different selective pressures promoting specialisation on each host.

It therefore seems to be the case that in the winter moth local adaptation to host-plant occurs either in cases where the range of available hosts is radically restricted (for example, as I alluded to earlier, in the *Betula* dominated forests of Scandinavia, or heather moorlands), or where gene flow is limited across great distances (i.e., isolation by distance; see Chapter 2). In the latter case, divergence may even simply signify the effects of drift. It has been suggested that female winter moths tend to ascend the same tree that they developed on as a caterpillar, and as such are capable of adapting to that individual host tree (Dongen *et al.*, 1997), though male dispersal would seem to act against this (van Dongen *et al.*, 1996). Such adaptation may still be possible if, like the larch tortrix, males also show preferences for individual trees, but there is currently no evidence to suggest this. Rather than adaptation at such a small spatial scale, we might expect instead—where individuals are unable to exercise discrimination in terms of the particular host individual that their offspring will end up on—that the mean phenology of a caterpillar population at a given site would match the mean phenology of the entire ‘host-plant population’ at that site, adjusted for the relative abundance of different host-plant species and their relative nutritional value. This would ensure, on average, a maximum amount of trophic match in any given year. Under such circumstances, therefore, we might not even expect to see ‘synchrony’ in the field at all, when comparing the phenology of any particular group of host-plants and individual caterpillars or broods—adjusted mean synchrony across a population will not necessarily present itself as synchrony at the level of particular individuals or particular broods. Such speculations are however yet to be fully investigated in the field, and would repay future enquiry.

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Appendix 11: Caterpillar rearing cultures

In the experiments described in this thesis, caterpillars were typically reared when neonates in (a) small 75 x 50 x 15mm transparent plastic containers. When large enough, usually in the third instar, caterpillars were transferred to (b) larger 175 x 100 x 50mm disposable plastic food containers. Rearing containers were lined with tissue which was replaced each time new food was added. When new food was added at one end of the container the old food was left in to allow caterpillars to move onto the fresh plant material as and when they chose. Similarly, (b) when caterpillars were transferred to larger rearing containers, the whole contents of the smaller container were moved, and new food supplied for caterpillars to move off onto as they chose. Scale bar in (a) is in centimetres and millimetres.